

AN ANALYTICAL STUDY OF THE CONDITIONED KNEE-JERK

BY
GEORGE RICHARD WENDT

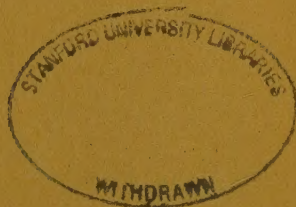
L. C.

Submitted in partial fulfillment of the requirements for the
Degree of Doctor of Philosophy in the Faculty
of Philosophy, Columbia University

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SECTION I. INTRODUCTION

Several studies of the conditioned knee-jerk in man have been published. The early studies of Twitmyer and of Shevaley have been followed by recent studies of the same phenomenon by Cornil and Goldenfoun and notably by Schlosberg. Switzer has made experiments on the possibility of backward conditioning of the knee-jerk. The interest of these investigators has centered in the possibility of setting up conditioned knee-jerks or in the study of the conditions of their formation. No systematic study of the characteristics of this response has been reported.

It was therefore the purpose of the present investigation to make an analytical comparison of conditioned knee-jerks with facilitation effects and with voluntary reactions. The data secured were to be graphic records from which the form and latency of the responses could be determined. The facilitating effect of the conditioned stimulus on the reaction to the unconditioned stimulus was studied on the theory that facilitation is but one aspect of the process involved in conditioning. Voluntary reactions were studied in order to compare their mechanism with that of the conditioned responses.

The method of the investigation in the production of conditioned responses was briefly as follows. Two stimuli were given at an interval of $1/5$ second. The first of these was a blow on the patellar tendon of one leg, eliciting a knee-jerk. The second was an equal blow to the patellar tendon of the other leg, also eliciting a knee-jerk. Repetition of such double stimulations of the two knee-jerks results in the formation of conditioned responses. The first stimulus alone then brings a response of the opposite leg. According to the accepted terminology, we may call the first blow the "conditioned stimulus," the second the "unconditioned stimulus." The response to the second is the "unconditioned response," while that to the first has customarily been called the "original response to the conditioned stimulus." The use of the two patellar stimuli has the advantages of (1) the possibility of several possible levels of integration in the development of conditioned responses, (2) an objectively recordable and exactly comparable response to both conditioned and unconditioned stimulus and

(3) relatively slight conscious representation of either stimulus or response.¹ The responses of each leg were recorded through the thickening of the quadriceps, the active muscle in the knee-jerk. All responses made by the subjects during the experimental sittings were recorded on smoked paper using a high-speed kymograph.

Three groups of results were secured. (1) Facilitation Effects. By a systematic variation of the stimulus interval, the facilitating (or inhibitory) effect of one blow on the response to the other blow was studied up to a stimulus interval of $\frac{1}{2}$ second. (2) Conditioned Responses. The genesis and characteristics of conditioned responses were studied in a number of subjects. Some subjects continued daily sittings over a period of three weeks during which up to 900 double stimulations were given. (3) Voluntary Reactions. The voluntary reactions of a number of subjects were studied as to form and latency under various conditions. A rapid kick of one leg, in response to a blow on the tendon of the other leg, was the prescribed voluntary reaction. Reactions to sound stimuli were studied for comparison.

The subjects were mainly graduate students in psychology and college students.

Details of apparatus and procedure appear in Section III.

¹ The use of the knee-jerk as a response avoids difficulties of interpretation involved in the use of nocuous or pleasant stimuli. In these cases the situation is frequently of the problem-solving type and, as a result, considerable "secondary elaboration" of the conditioned stimulus may be assumed to take place. The removal of the motivational element seems desirable in analytical work on the conditioned response in humans.

SECTION II. THE REFLEX MECHANISM

The stimulus for the knee-jerk is the stretching of the quadriceps muscle resulting from the sudden deformation of its tendon by a blow. The afferent impulses arise from the receptors within the muscle when it is submitted to stretch or tension. The afferent fibres run in the crural nerve, the efferent fibres run in the same nerve. The latter have their origin in the second to fourth lumbar segments.

The response is a rapid contraction of the quadriceps, certain of its constituent elements—vastus internus and vastus medialis—being chiefly involved. Associated with the extensor contraction there is known to be a reciprocal relaxation of the flexors of the leg and probably contraction of other muscle groups. The latency of the reaction is among the shortest of the reflexes. Travis and Young find the current of action to begin on the average 18.9 sigma after the tap on the tendon, with slight individual variation (S.D. = 1.76 sigma). When the response is recorded by the thickening of the muscle, as was the case in the present investigation, the first observable change in the muscle takes place at a considerably longer interval (30 to 50 sigma). The latency of the response as recorded by muscle thickening shows greater variability between individuals, probably because of peripheral factors.

Because of the short latency of the knee-jerk, it was thought by Westphal (co-discoverer, with Erb, of the knee-jerk) and by his followers that the response was not reflex but an idiomuscular reaction to mechanical stimulation. This view has been displaced by a recognition of its reflex nature as urged by Erb. The majority opinion at present regards the knee-jerk as a local spinal reflex having its arc within the segment of the entry of the afferent nerves. Opposed to this is the view that the knee-jerk has its discharging center at some point higher in the neural axis, in the medulla, midbrain, or higher centers. The level of the arc involved in the knee-jerk is not of paramount interest to this investigation which is concerned with the level of discharging centers only insofar as they may be revealed by *relative* latencies of different kinds of responses. Whether physiology accepts the doctrine of "long-circuiting"

of the tendon reflexes can have no effect on the validity of the present results nor on their general interpretation.

However, several researches seem to indicate that the knee-jerk is not a simple response in which but one discharging center is involved. The knee-jerk has a rapid or clonic phase and then relaxes more slowly in the tonic phase. In infancy and in total transverse lesions of the spinal cord in man the knee-jerk consists of a single rapid twitch, lacking the tonic phase. Recent papers by Travis and Hunter and by Travis, Tuttle, and Hunter presenting studies of action currents during the knee-jerk indicate that there may be two discharging centers operative. All results showing facilitation of the knee-jerk by concomitant stimuli or activities point to the participation of more than one level. The cooperation of centers having a longer latent period of discharge is a possibility of considerable importance in considering the integration of the two knee-jerks into a new pattern. It is an indication of the activity of higher levels which may be necessary to the integrative processes.

Other stimulation in addition to the afferent impulses set up by the muscle stretch was, of course, present in this experiment. Visual and auditory cues signalling the arrival of the blow were eliminated, but the blow to the knee gives rise to a diffuse tactual-kinesthetic stimulation of which the muscle stretch is but one element. This involves the touch on the knee, the pressure on the tendon and underlying tissues and a slight jar to the whole body. These aspects of the stimulation may be of especial importance when working with the present stimulus pattern.

The first question which arises in connection with the type of stimulation here used is whether there is not normally an integration of the reaction of the two quadriceps muscles. Since the researches of Sherrington (1893-1909) the allied action of reflexes has been a major interest of neurophysiologists. The wide interaction of reflexes has by this time been sufficiently demonstrated. Perhaps the most familiar example of an allied reflex is the "crossed extensor" studied usually in decerebrate preparations. Nocuous stimulation of the foot causes flexion of the leg and extension of the opposite leg.

In the present instance there is a strong possibility of allied reaction. Neurologists daily use the presence of certain

allied reflexes as diagnostic of lesions of the central nervous system. These conditions go by the various names of associated movements, associated reflexes, paradoxical reflexes, crossed reflexes, etc. They appear most commonly in affections of the pyramidal tracts.

The associated movements are defined by Walshe (*Brain*, 1923) thus, ". . . associated reactions are evoked most typically by voluntary tonic contraction of muscles. They are not produced by rapidly alternating movements unless these are wide-spread or forceful, and they cannot be produced by cutaneous stimuli apart from such tonic contraction. In short, the adequate stimulus is proprioceptive and of some duration. The response has a comparatively long latent period (0.25 to 2.0 seconds), is commonly slow in development, and lasts, or may outlast, the duration of the stimulus." Among these associated reactions, leg extension is common. However, the character of these movements associated with forceful voluntary or automatic activity is essentially different from the reactions here investigated. They differ not only in stimulus, but also in latency and form.²

Austregesilo states that "In the association of reflexes, to one stimulus only two or more reflexes respond, . . ." Thus, to a blow on the patellar tendon there may be elicited not only a knee-jerk, but also vigorous contraction of the biceps and a crossed reflex (usually adduction) of the other leg. Certain reflexes are regularly found associated in conditions of hyper-reflexia or in cases of pyramidal lesions. When the association is unusual or anomalous, the response is known as a paradoxical reflex. In the case of the paradoxical reflex the response proper to the eliciting stimulus may be lacking, and some other response be made.

Under the conditions of the present investigation there is the possibility of experimentally producing a crossed reflex. This crossed reflex, if like the original response, would be leg extension as in the knee-jerk.

Crossed reflexes have frequently been reported in man and

² The best discussions of associated movements will be found in the papers of Walshe listed in the bibliography. For another view of them see paper by Brock and Wechsler. These papers refer to a wide literature on the subject.

are well-known clinical phenomena.³ The crossed reflex of interest to us, that is most frequently found in the clinic, is that of adduction of the opposite thigh on percussion of the patellar tendon.⁴ A slight crossed adductor jerk is present in many normal individuals but pronounced cases are usually found only in affection of the pyramidal tracts.* In man, action current records show the response to have a latency even shorter than that of the knee-jerk. Schäffer reports a value of 19 sigma determined on three patients with crossed adductors, while Wegener finds even shorter latencies of 11 and 13 sigma. Stewart, a much earlier investigator, reported latencies measured by the beginning of muscle thickening. He found an average of 126 sigma to elapse before the response began. However, his technique was not without faults, and it is possible that he was not measuring the latency of crossed adduction but of crossed extension associated with it. The general belief of neurologists seems to be to the effect that the crossed adductor reflex has a level of action similar to that of the knee-jerk. Its presence in spinal dogs and in spinal monkeys is a prominent result of this condition, but in spinal man it is not ordinarily observed, though the knee-jerk may be brisk.⁵

An associated *crossed extensor* response to percussion of the patellar tendon would be of paramount interest to the present investigation. Such a response has been infrequently reported. Schwarz (1882) reported a case of a paradoxical crossed extensor (with absence of the homolateral response), and Austregesilo mentions Benedikt as reporting a similar case. Gotch (1896) reported response latencies in a case ex-

³ Early papers reporting crossed reflexes are: Schultze and Furbringer, *Ctb. f. med. Wissensch.*, 1875, 13, 929-932; Westphal, *Arch. f. Psychiat. u. Nervenkr.*, 1875, 5, 803-824; Gergens, *Pföger's Arch.*, 1877, 14, 130-134; Erlenmeyer, *Ctb. f. Nervenheilk.*, 1880, 3, 345-350; Prevost and Waller, *Rev. med. de la Suisse Rom.*, 1881, 1, 347-352; Schwarz, *Arch. f. Psychiat. u. Nervenkr.*, 1882, 13, 621-657; Strümpell, *Arch. f. klin. Med.*, 1890, 47, 53-74; Waller, *J. Physiol.*, 1890, 11, 384-395; Eichhorst, *Ctbl. f. klin. Med.*, 1892, 13, 641-642; Sternberg, *Die Sehnenreflexe*, etc., 1893, pp. 180-181 (Sternberg refers to other papers not listed here); Marie, *L'Union Med.*, 1894, 57, 524-525; Hinsdale and Taylor, *Inter. Med. Mag.*, 1894, 4, 369-376; Russell, *Amer. J. Med. Sci.*, 1896, 111, 306-313; Gotch, *J. Physiol.*, 1896, 20, 322-333; Stewart, *J. Physiol.*, 1897, 22, 61-67.

⁴ For excellent discussions of the crossed adductor jerk see the papers by Austregesilo and by Wegener.

⁵ For a description of the state of the reflexes after complete transection of the spinal cord in man see the full description given by Riddoch. The review by Horax refers to other papers.

* The present apparatus prevented lateral leg-movement.

hibiting a crossed extensor, finding an average latency for the beginning of muscle thickening of 110 sigma. There was some evidence in his records that the discharging center active in the crossed extensor had a bilateral action. Souques and Chauvet (1912) also noted a case of vigorous crossed extension to a blow on the patellar tendon. They found this response to come a little later than the homolateral response. Tuttle (*J. Exper. Psychol.*, 1925) reported a subject with hyperexcitable knee-jerks though otherwise normal in whose case vigorous crossed extension followed blows to the patellar tendon. The amplitude of the crossed reflex was found to vary with and be almost equal to that of the homolateral response. On the whole, crossed extension does not seem to be a frequent occurrence, though it is occasionally noted in clinical reports. It is overshadowed by the more frequent crossed adductor jerk.

Though further reports of crossed extensor responses in normal individuals have not come to the attention of the writer,^{5a} it seems probable, from the occasional presence of such an alliance in abnormal conditions, that we may expect to find the integrating paths from the receptors of one side to the contralateral effectors of relatively low resistance.⁶ Even though direct reflex connections between the two should be lacking, integration on higher levels could be close. Sherrington states (1906) that "In the presence of the great proprioceptive receptors and the brain there can be few receptors in the body whose activities are wholly indifferent to one another." p. 147.

^{5a} It is possible that under normal conditions of locomotion a stimulus for the knee-jerk may result in crossed extension due to the summative effect of impulses set up by general activity. The lack of such summation in experimental situations may explain the absence of crossed response.

⁶ This type of stimulus-response situation in conditioning studies is not new. Cason (1922) used a sound as a conditioned stimulus for the lid response. The lid response is closely allied to the sound stimulus.

SECTION III. APPARATUS, GENERAL METHODS AND SUBJECTS

General Description

During the experimental sitting the subject sat comfortably reading in an arm-chair, screened from the room and the apparatus by high sides built onto the chair. His legs hung over padded leg-rests, swinging free during the jerk. Records of the thickening of each quadriceps were transmitted by two identical levers and pulley systems to a high-speed motor-driven kymograph. All responses were recorded throughout the ex-

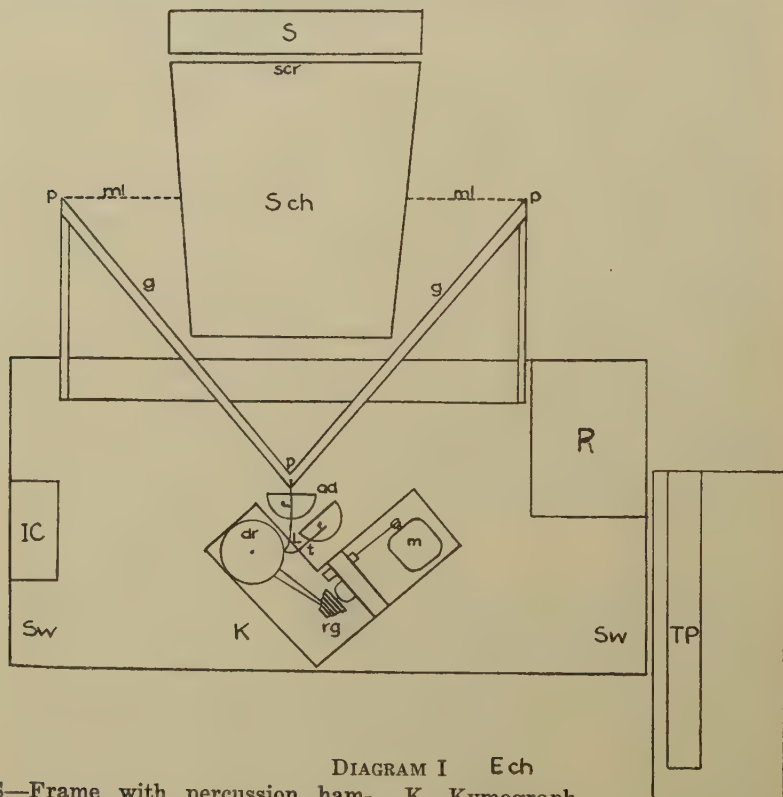


DIAGRAM I E ch

- | | |
|------------------------------------|------------------------------|
| S—Frame with percussion hammers. | K—Kymograph. |
| S ch—Subject's chair. | m—Motor. |
| scr—Screen. | rg.—Reducing gear and brake. |
| ml—Muscle levers. | dr—Drum. |
| p—Pulleys for recording lines. | ad—Adjustable stands. |
| g—Glass tubes for recording lines. | L—Recording levers. |
| R—Relays, etc. | t—Tuning-fork. |
| IC—Induction coil. | TP—Timing pendulum. |
| Sw—Switches, etc. | E ch—Experimenter's chair. |

perimental period. Time was recorded by a 50 d.v. tuning-fork. The stimuli were provided by two stimulating hammers of the gravity pendulum type released from magnets by means of a device which gave easy control of the stimulus interval. Sound cues incidental to the apparatus and the blow on the leg were eliminated by the use of ear-phones in which a constant loud buzzing noise was produced. See diagram I for the arrangement of the various pieces.

Detailed Description

a. The subject's chair:—A heavy, unpadded wooden arm-chair was changed by the addition of a back and two sides of wall-board which came to a height of 30 inches above the seat. A front screen was removable so that, with the subject in position, it could be replaced. The screens cut off the subject's vision for all parts of the room except adjacent to the ceiling. The removable front screen was provided with a shelf to hold reading matter. The subject's legs were slightly elevated by leg-rests which were adjustable for height and for length. Pads prevented lateral movements of the legs. The legs were at all times permitted to swing free during the jerk. This method was thought advisable because the experimental sittings lasted one hour. If the legs are not allowed to move, the stoppage of circulation makes the subject very uncomfortable.¹

b. The recording system:—In order to secure muscle thickening records from each leg with lever systems as nearly identical as possible, it seemed best to place the kymograph behind the subject and to use a comparatively long lever and pulley system. A light wooden lever rested on each muscle at a point about $\frac{2}{3}$ of the distance from the attachment to the patellar tendon. Its length was 19 inches. Its contact with the muscle covered some space along the muscle so that the fulcrum (a knife-edge joint) was 8 inches from the center of the muscle. The outer end of the lever projected 10 inches beyond the fulcrum. Two close-wound coil springs (a small one within a large one) were attached to the lever between the fulcrum and the point of contact with the leg. The lever was adjustable both for position along the thigh and for height. A thumb-nut on the outer end of the lever allowed the rapid adjustment of the pulley system which connected with the recording levers. By means of a 50 inch length of hard-braid, 20 pound test silk casting-line (stretched to reduce elasticity) running over two fine pulleys, the movements of the muscles were transmitted to the writing levers at the kymograph. From their attachment at the muscle levers each line ran up 10 inches to a very light pulley with steel needle-point bearings running on brass. After passing over these pulleys they stretched 36 inches diagonally to the rear to a common point just behind the subject where, after passing under two pulleys similar to the others, they attached to the recording levers. Each recording line was shielded from air currents by an enclosing glass tube. The writing levers were 7 inches long with knife-edge fulcrums 4 inches from the writing end. The levers were of iron wire. A fine coil spring attached to each kept the whole system under tension. The levers were mounted on an adjustable stand so that the points could rapidly be brought against the drum surface. This recording system gave some magnification of the muscle thickening (1 : 1.7).

The faithfulness of the obtained records to the changes in the muscle was checked by measuring the transmission-time of the recording sys-

¹ Schlosberg notes that the conditioned responses of the free-swinging leg are of greater amplitude than in isometric contraction.

tem. The moment of contact of the hammer with the tendon was registered by means of a contact at the knee and a signal marker. Some time is necessarily lost in the transmission. With the present recording system the movement of the recording lever was found to follow the depression of the signal marker by about 5 sigma. This loss would balance for each recording system, so would not affect the results. The form of the curve of contraction was very likely affected to some extent by the inertia of the system and by the slight elasticity of the transmission line. That there was no serious modification of the form of the curves was indicated by their close similarity to those gotten during preliminary work with direct recording levers. Slight distortion due to the friction at the smoked paper surface was probably present. The friction at the pulley bearings was negligible. There was also, of course, distortion due to the fact that recording levers of the kind used do not move straight up and down but describe an arc. With a reflex of normal magnitude this factor is not of great importance.

c. The kymograph—A special kymograph was arranged making possible a large number of records at high drum-speed during a single sitting. The drums were of the conventional type (6 inches diameter, 6 inches in height) mounted on a vertical $\frac{3}{8}$ inch shaft. The motive power was a $\frac{1}{25}$ h.p., d.c., series wound motor with a speed rating of 1800 r.p.m. This was belted to a Fisher reducing gear, and this in turn belted to the kymograph shaft from a cone pulley at the reducing gear to another cone pulley on the shaft. A brake was arranged so that its release started the motor. Setting the brake broke the motor circuit. This arrangement allowed of high drum-speeds with no record wasted during acceleration or stopping. Three to nine drums were used during an hour, depending upon the drum-speed. The speed could be varied over a wide range by means of the cone pulleys. Speeds of from 3 to 8 inches per second were used, most of the records being taken with a speed of $5\frac{1}{2}$ inches per second. Drum changes were very easily made, the whole operation taking but 15 seconds.

d. The tuning-fork—A 50 d.v. tuning-fork mounted on a separate adjustable stand wrote on the record between the two lines for muscle thickening. It was checked for accuracy at the beginning and at the end of the investigation.

e. The percussion hammers:—Two percussion hammers of the gravity pendulum type were mounted on a separate wooden frame. The hammer shafts were brass tubing, the heads were balsa wood. Graded lead weights could be attached to the rear of the head. Two cut-down telegraph keys furnished excellent pivots from which to swing the shafts. The hammers swung 10 inches apart. From the pivot of the hammers to the striking surface of the heads was $17\frac{1}{4}$ inches. They were held by magnets (taken from relays) attached to arms adjustable for any angle of fall. Throughout the experiments this angle was 45 degrees.⁸ When the heads were weighted with 150 grams of lead (the weight of the hammer alone was 170 grams), the time of the swing to the leg was 0.32 seconds. The weighting of the hammers was either with 100 or with 150 grams, depending on the sensitivity of the subject. The cores of the release magnets met on each shaft with a strip of wrought iron.

Upon striking the tendons there was always a strong rebound of the hammers which would give two or three additional blows to the tendons unless stopped. To prevent this, strong magnets were so arranged as to catch the hammers on the rebound. Each was arranged as follows: The essential parts were the catching magnet, two relays, a mercury-cup break contact controlled by the falling percussion hammer and a contact key. So long as the percussion hammer was in the raised position the mercury-cup circuit was closed; just before the hammer reached the knee

⁸ Dodge (1911) notes that the effect of changing the speed of the hammer and of changing its weight is not the same.

it was opened. This circuit activated the magnets of the two relays, but was also run through the secondary circuit of one of them (relay 1). The circuit activating the catching magnet was run through the secondary circuit of the other relay (relay 2). The break of the mercury cup contact by the down-swing of the percussion hammer closed the circuit of the catching magnet controlled by the secondary circuit of relay 2. At the same time the secondary circuit of relay 1 was opened. The opening of this contact prevented the reactivation of both relays on the rebound of the hammer (which once more closed the mercury-cup). Hence, the hammer stayed at the magnet until released by the manual depression of a contact key "shorted" across the secondary points of relay 1, which reactivated the relay magnets and broke the circuit in the catching magnet. In over 21,000 falls of the hammers this mechanism did not fail to function.

The hammers were pulled up to the releasing magnets by hand. A light braided silk line attached to each hammer shaft led through a glass bearing and then through three glass-lined guides (to reduce friction affecting the fall of the hammer) to the experimenter's table.

f. The stimulus interval:—The circuits of the releasing magnets were broken by means of a heavy pendulum which broke two mercury contacts as it swung through its arc. The pendulum bob weighed seven pounds. It swung through its full arc in one second. It was released from an angle of 25 degrees. A track built in the form of an arc supported the two movable break contacts. On its initial swing the pendulum opened these and on its return swing it closed them. The pendulum was released by manually depressing a spring catch, it then swung through its arc, returned, and was caught by a second spring catch. Lifting it slightly returned it to its original position ready for the next stimulation. This arrangement gave easy and rapid control of the stimuli. It was possible to reset both percussion hammers, change the time interval between stimuli, reset the time interval pendulum and release it for the next stimulation so quickly that less than 15 seconds need elapse between stimuli. Two double-pole, double-throw switches saved additional time during the study of facilitation effects. By means of these either of the break contacts at the timing pendulum could be made to release either of the percussion hammers. Thus each order of the stimulation (left-right or right-left) could be given at one setting of the contact points on the timing pendulum.

The constancy of the stimulus interval might be affected either by variations in the circuit-break at the timing pendulum or by variations in the fall of the percussion hammers. The latter factor seems to have been of relatively slight importance. The error due to the time of break was relatively greater for the smaller intervals (simultaneity to 60 sigma), though the absolute error here was least. The settings for the small time intervals were at the center of the arc of the pendulum swing where its velocity was greatest. With simultaneous stimuli the variation in each direction was estimated from the time records to have been not much over one sigma in each direction. At the $1/5$ second interval it was not over three sigma. When accurate measurements were required the stimulus incidence was always determined directly from the records.

g. The sound "Screen":—Secondary sound cues came from three sources. (1) The timing pendulum made a slight noise as it broke the contacts. (2) The motor of the kymograph produced considerable noise. (3) The impact of the percussion hammers with the knee produced a thud and a slight rattle of the pivots of the hammers. Although the first two factors could have been largely eliminated, the last-mentioned cannot be wholly prevented with this type of stimulation. It was therefore necessary to remove sound cues by producing such intense noises as to smother all other sound. The subject was provided with ear-phones through which the output of an induction coil was sent. This produced a noise easily made loud enough to smother all sounds connected with

the manipulation of the apparatus.⁹ For the greater comfort of the subject his ears were stuffed with cotton and a folded handkerchief placed between each ear and the phones. This helped prevent sound leakage and made possible the use of a noise which, relative to the external sounds, was much more intense than would otherwise have been possible. Although the sound was distinctly unpleasant to the subjects at first, they rapidly became adapted to it.

h. Accessory apparatus:—Since most of the subjects served during the hot months of June, July and August, an electric fan was placed above the chair.¹⁰

By means of other switches, relays, signal markers, etc., the apparatus was arranged for the study of conditioned responses or voluntary quadriceps responses to (1) a sudden click, (2) a prolonged buzz, (3) the onset of silence after a continuous buzz, (4) a single or prolonged electric shock, (5) a touch stimulus to the leg below the knee. Any of these could be used in connection with a blow to the knee at intervals up to one-half second.

General Arrangement

Reference to Diagram I shows the general arrangement of the apparatus. The work was done in a 9' 8" by 13' 6" room with a large window behind the experimenter. This, together with a ceiling light, furnished the subject with good illumination for reading. The floor was cork laid over concrete and would not easily transmit vibrations. The subject's chair was in contact with no other part of the apparatus except by means of the silk recording lines, thus eliminating all vibratory stimuli from the apparatus.

General Method

In brief, the general procedure was as follows. Having removed coat and shoes the subject sat back in the chair with his back firmly against a leather cushion in order to prevent backward movement of the whole body during the swing of the leg. The front screen was put in place and the subject given reading matter.¹¹ The leg rests were adjusted for length and for height so that the percussion hammers swung just at the center of each tendon. The percussion hammer frame was then exactly adjusted. The muscle levers were inserted through an aperture in each side of the chair and adjusted to the setting determined for the particular individual. All records were taken through the clothes covering the thigh. The lines leading to the writing levers were then adjusted until both levers were horizontal when the leg was at rest. The ear-phones were adjusted and the sound increased to the limit which the subject found tolerable. He was then instructed to read, giving all his attention to the reading and none to the experiment. The importance of complete distraction of the attention was emphasized. The percussion hammers were then raised, the time interval pendulum set and the writing points adjusted against the kymograph drum. After a short wait for adaptation the stimulations were begun. The timing pendulum was released, a fraction of a second later the kymograph was started, then the brake of the kymograph was set as soon as the knee-jerks had recorded. With practice it was possible regularly to get the first jerk recorded 1/10 to

⁹ Jenkins (*Arch. Psychol.*, No. 86) found that reaction-time to light was reduced by the presence of continuous sound. It is questionable, however, whether the presence of the sound in the present investigation had a facilitating or soporific effect.

¹⁰ Hot weather reduces the knee-jerk (Lombard, 1888) while cold weather increases it (Emery, *Am. J. Physiol.*, 1925 and Miles, *Proc. 9th Intern. Cong. Psychol.*, 1930).

¹¹ Current popular periodical literature was provided. Jacobson (1928) reports that the effect of prolonged reading is a reduction in the amplitude of the knee-jerk due to relaxation. The present subjects became very comfortable and relaxed, so we may assume a general depression of the knee-jerks from this cause.

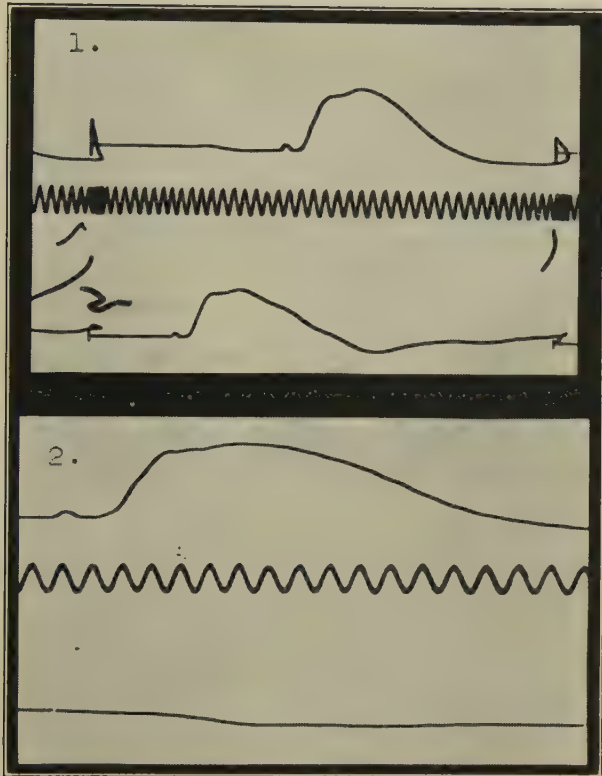


PLATE I. Typical records of knee-jerks. (1) Lower line is left quadriceps, middle line is 50 d.v. tuning-fork, upper line is right quadriceps. The drum speed is about 3 inches per second. The figures on the record indicate the intervals between double stimulations. (2) A facilitated jerk of the right leg. Drum speed about $8\frac{1}{2}$ inches per second.
 Note: The reproductions are "negatives."

1/5 second after the drum started and to stop the drum in a little more than $\frac{1}{2}$ second. Resetting the hammers and pendulum made the apparatus ready for the next stimulation.

Measurement of the Records

The records of normal knee-jerks obtained by the use of this apparatus (see Plate I for jerks to two paired stimuli) presented the following characteristics. The resting line of the muscle is a straight line parallel with the lower edge of the kymograph paper, (so long as this is accurately applied to the drum). The blow to the leg gives rise to a sudden disturbance of the muscle which records as a small sharp rise of the line, returning to the baseline within 20 sigma. Small oscillations may occur after this return (See Dodge, 1911). The initial rise due to the stimulus is followed, after an interval, by a rise caused by the reflex thickening of the muscle. The interval from the beginning of the first rise to the beginning of the second is the reflex latency. As the muscle thickens the line rises first slowly and then steeply. A depression near the top of the rising wave is present in most of the records. The contraction rapidly reaches its crest and then begins to fall away. The relaxation is slower than the rising phase. It usually falls below the resting line and returns above it again in a second rise. Further slow oscillations related to the swings of the leg are often present. The part of the curve following the dip below the base line was of no interest to this investigation and in most instances does not appear on the records, since the drum was stopped before it was reached. The second rise is very likely due partly to an effort on the part of the subject to control the swing of the leg, and partly to reflex impulses set up by the stretching of the muscle as the leg falls. The temporal incidence of these rises is outside the limits of the phenomena studied in the present investigation.¹²

The latency of both homolateral and crossed contraction of the muscles could be determined by lines perpendicular to the edge of the kymograph paper drawn (a) through the point where the line first left the base line after the blow and (b) the point where the line first left the base under reflex contraction. The time determination is subject to error in (1) the determination of the point of the beginning of muscle thickening and (2) the reading of the time values from the tuning-fork oscillations. The first error can be reduced only by the use of greater magnification or by practice in reading the records. The second is reduced by increased drum speed. The number of tuning-fork oscillations between the two perpendiculars was counted and the time estimated in units of one sigma. Accuracy of estimate in the order of one sigma is of course impossible with such a slow tuning-fork, but it is safe to assume that the results would not be markedly affected by the use of a faster instrument.

Subjects

Twenty-nine people (five women, twenty-four men) served as subjects for varying periods of time. Twenty-two were graduate students in psychology, four were college students, two were in outside employment and one was in high school. The last-named was aged 16, one was aged 35, all the others were between 21 and 29 years of age. Of the college students three were paid for their time, since their services were required daily for three weeks. Although it is not regarded as a matter of any importance, it may be stated that but one of the subjects had any clear conception of the purpose of the experiment, and most of them had none.

Of these subjects 23 gave data on facilitation effects, 17 on conditioned responses, 16 on voluntary leg reactions to a blow on the opposite patellar tendon, 10 on voluntary leg reactions to sound and 1 on voluntary leg reactions to a touch stimulus.

¹² Travis, Tuttle and Hunter (1927) discuss the temporal incidence of the discharge causing these contractions.

SECTION IV. FACILITATION AND INHIBITION EFFECTS

That the amplitude of the knee-jerk may be augmented by a preceeding or accompanying stimulus has been reported by many investigators.¹³ Among the sensory stimuli which may increase the response are sudden sounds and noises, sudden lights or other visual stimuli, various cutaneous stimuli such as touches, pinching the skin, sudden heat or cold or sudden currents of air, vibratory stimulation as of a slow-tuning-fork held against bone and the passage of an electric current. Mental work, all stimuli arousing interest or emotions and any strong emotion have been found to have a heightening influence. Movements of any kind are especially effective as reinforcing agents. Voluntary or reflex movements, effort, sneezing, coughing, yawning, deep breathing, hunger contractions and other factors have been reported. Electrical stimulation of afferent nerve trunks gives rise to marked facilitation.

That the amplitude of the kick may be reduced under various conditions is also well-known. Any condition which leads to relaxation leads also to reduction of the reflex. In sleep it is slight or absent. During voluntary relaxation it may become much reduced. Prolonged reading, writing or copying will cause reduction if they result in relaxation. The same is true of pleasurable stimuli leading to a reduction of effort. Giving word associates to unpleasant words seems to have a similar affect. Hot weather, fatigue, and hunger are depressing factors.

A second group of factors reduce the knee-jerk through an active inhibitory effect. Most prominent among these is painful stimulation. A painful stimulus preceding the blow reduces the response, while persistent pain may give rise to generalized hyporeflexia. Other active factors in reducing the knee-jerk have not been clearly defined. It is familiar to clinicians that distraction of the attention will frequently make it possible to elicit a knee-jerk in a patient otherwise without one. It is thought that this is due to the inhibitory

¹³ For recent reviews on facilitating and inhibiting influences on the knee-jerk see Jacobson (1929) Ch. 14 and Fearing (1930) Ch. 15.

effect of the higher centers on the reflex. The nature of this action is not well-understood.

Though voluntary activity reinforces the knee-jerk, it has also an effect in reducing it. A period of post-facilitatory depression was described by Bowditch & Warren. They showed that when a voluntary act preceded the blow on the tendon by an interval of 0.22" to 0.6" (for different subjects) the resulting kick was augmented. In some subjects this was followed by a period of decreased activity up to an interval of 1.7 to 2.5 seconds when the extent of the jerk returned to normal. Russetzki (1928) has made similar observations.

It is therefore to be expected that the blow on the patellar tendon of one leg will have some effect on the reaction of the other leg. It is probable that the mechanism of facilitation (and of conditioning) rests on the convergence of afferent pathways at some common points in the central nervous system. A knowledge of the temporal incidence of the effects seems essential in order to know what levels of integration (inferred from the temporal relationships) may be possible in conditioning. The time relations of the facilitation effects may be expected to appear also in the conditioned responses. The purpose of the facilitation experiment was to make an exploratory study over a range of stimulus intervals. Evidence of the effects was obtained on a main group of 6 subjects with collateral evidence from 17 other subjects.

The procedure for the main group of subjects was as follows. The general arrangement and the general method were as described in Section III, secondary sound cues being eliminated by the use of ear-phone noises. The presence of secondary sound cues makes tests for facilitation effects unreliable because the subject may become conditioned to the sound and react in anticipation of the blow to the knee. The experimental sittings lasted for 50 minutes during which 96 stimulations at one-half minute intervals were given. In 72 of the stimulations both tendons were struck while 24 were single stimulations (12 of the left tendon and 12 of the right). In the double stimulations 9 intervals were used, each occurring 8 times during an experimental sitting, with the blow to the right leg preceding in 4 cases, the blow to the left leg in 4 cases—all in a random order which was changed 4 times during each experimental sitting. The intervals used were: 0, 10, 20,

40, 100, 150, 200, 300 and 500 sigma. In all cases the determination of the time interval between paired stimuli was directly from the records which were taken with a high drum-speed. As was noted in Section III, there was some variability in the incidence of the stimuli at any one setting of the timing pendulum. It is unlikely that this affected the major results obtained. Since the amplitude of the response of each leg was recorded, it was thus possible to test the effect of a blow on the opposite leg intercurrent on the contraction of one leg.

Four of the main group of subjects served on the same hour on four consecutive days; two served for only three days.

The results are presented in terms of percentage of normal amplitude. The facilitated jerks at each stimulus interval are compared to the normal jerks for the whole period in terms of per cent. The final result is gotten by averaging the results of each leg computed separately.

The average normal (unfacilitated) amplitude of the jerk of *each* leg was first separately computed. For these averages the 12 single jerks in each sitting were used together with the amplitudes of the first jerk of each pair in the double stimulations at the intervals 150, 200, 300 and 500 sigma. At these intervals the first jerk of the pair has passed its crest by the time the contralateral blow falls and its amplitude cannot be affected by it. This gave 28 daily normal jerks for each leg, or a total of 112 for each leg with the 4-day subjects and 84 with the 3-day subjects.

In the computation of the amplitude of the test jerks there were two groups of results, according as the contralateral blow fell before or during the test jerk. For the computation of the latter group the amplitudes of the first of each pair of jerks were separately averaged for each leg at the intervals 10, 20, 40 and 100 sigma. For the computation of the group where there was a preceding stimulus the amplitudes of the second of each pair of jerks were separately averaged for each leg at all the intervals from 10 to 500 sigma. For the simultaneous combination the amplitudes of the right and left jerk were separately averaged.

To find the amount of facilitation at any interval it was then necessary to express the average amplitude of the test jerks as a percentage of the normal jerk. This was separately done

for the left and the right leg. To achieve the final result these two percentages were averaged for each interval. The final result thus gives in per cent the relative amplitude of the test jerks as compared to the normal. Percentages below 100 indicate a depressing effect, percentages above 100 indicate an augmenting effect. Each final determination rests on the comparison of 32 test jerks with a normal averaged from 224 knee-jerks. (For the 3-day subjects the figures are 24 and 168.) The simultaneous combination is an exception to this, being determined from twice as many tests.

RESULTS OF THE MAIN GROUP

The presence of a facilitation effect is clearly shown in the results. The combined results of the six subjects are presented by the curve in Figure I. Values along the Y-axis are amplitudes in per cent of normal. Values along the X-axis are stimulus intervals. Amplitude values above the X-axis show augmentation, those below show reduction in the amount of muscle thickening. Points on the left of the Y-axis represent average amplitudes of the first of the paired responses when followed by a blow on the other leg at intervals up to 100 sigma. Points on the right of the Y-axis represent average amplitudes of the second of the paired jerks. Table I contains the values for each subject from which the curve was derived. The composite curve shows that *the main facilitating effect has begun at a stimulus interval of 100 sigma, is maximum when the interval is 150 sigma, with 200 sigma is still strong and has practically disappeared at the 300 sigma interval. At the 500 sigma combination there is evidence of lessened excitability.*

TABLE I
FACILITATION EFFECTS

Subj.	Contralateral st. follows				Stimulus interval in sigma								Contralateral st. precedes			
	100	40	20	10	0	10	20	40	100	150	200	300	500			
Gol	97	105	96	102	77	110	129	121	269	341	241	194	115			
Jac	88	103	102	83	81	105	122	86	160	210	165	99	103			
Smi	58	100	78	82	67	88	115	114	162	164	136	119	95			
Dur	104	99	100	113	87	101	98	92	102	188	152	83	61			
Mac	114	114	97	100	91	110	154	116	75	90	124	91	88			
Harr	100	105	100	100	93	104	102	103	81	84	84	82	79			
Av	93	104	97	97	82	103	120	105	142	180	150	111	90			

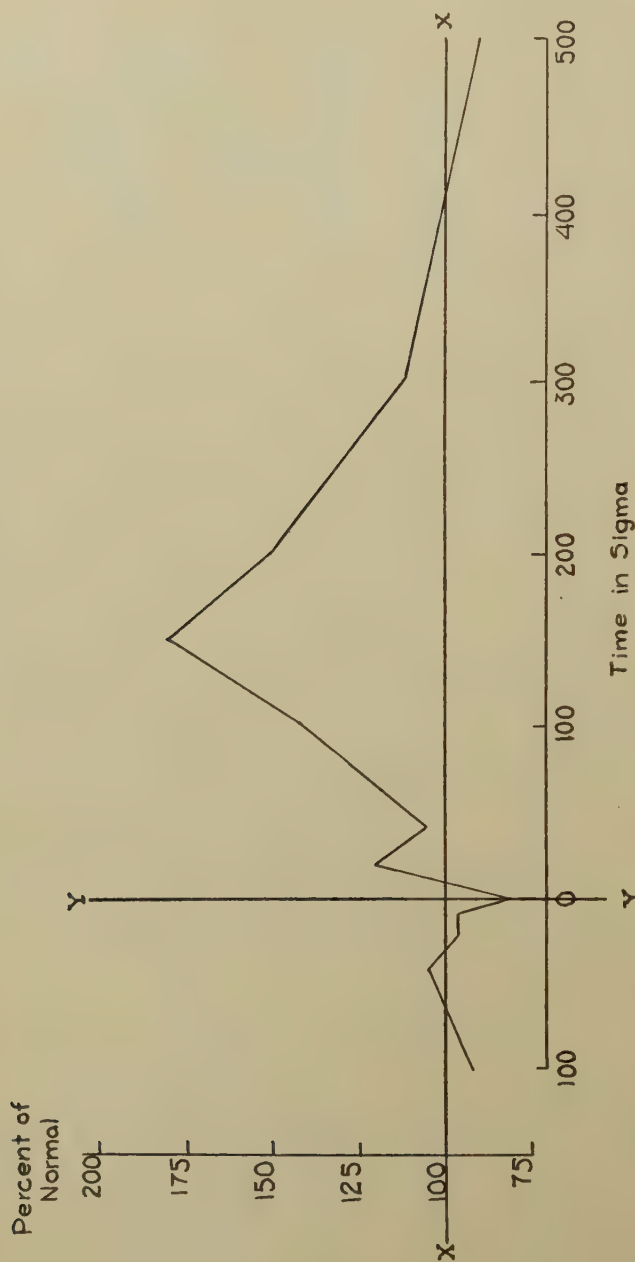


FIGURE I. FACILITATION EFFECTS (SIX SUBJECTS).
Values to left of Y indicate amplitudes of the first of two paired responses. Values to right of Y indicate amplitudes of the second of two paired responses.

Reference to the results of each subject shows that individual differences in the effects at these intervals were considerable. A careful analysis of the results of each subject must be made in order to make any statements about the reliability of the figures at any one interval. Taking into account the normal variability in each case and the general excitability of the knee-jerks, analysis shows the following results.

a. One subject (Gol) showed facilitation from 100 to 300 sigma stimulus interval with no significant deviation from normal at 500 sigma.

b. Two subjects (Jac and Smi) showed facilitation from 100 to 200 sigma with no significant deviation from normal at 300 and 500 sigma.

c. One subject (Dur) showed facilitation only at 150 and 200 sigma, while at 300 and 500 sigma there was reduced excitability of the jerk.

d. One subject (Mac) gave no consistent results though the main effect was inhibitory.¹⁴

e. One subject (Harr) showed inhibition at all intervals beginning at 100 sigma.

Separate analysis of the facilitation effect for the right and left leg of each subject gives the same results.

When the curve is inspected at the shorter time intervals, it is seen that there are but two points which show a noticeable variation from normal. When the hammers struck simultaneously, both kicks were on the average slightly subnormal. When the stimulus interval was 20 sigma, the second jerk was slightly augmented on the average. The depression with simultaneous stimulation was true of each subject and for each leg of each subject computed separately. The computations for this combination are based on twice as many test jerks as the computations for the other combinations. Because of the difficulty of interpreting such a reduction without further experimentation, and because it seems to have no relation to the conditioning process, it will not be further discussed. The increase at the 20 sigma interval was present in four of the six subjects. Its inconstancy within the results of

¹⁴ This subject's knee-jerk was slight and often absent. A football injury to the patella sustained some years before may have affected the results.

the individual subjects makes it possible that it was a chance variation.

Collateral Results

Table II gives collateral results from 17 subjects. The results of the first six in the table were obtained by essentially the same method as in the main group of subjects but the number of trials was in some cases less and the stimulus intervals used were not the same. Only the amplitudes of the second of the paired responses are given. The results of the last 11 subjects in the table were computed from amplitudes of response during conditioning trials. The norms of response were obtained from the presentation of the second of the two blows alone several times during the hour. The number of jerks on which the norms were based varies from 6 to 55 in these cases, while the available facilitated jerks varied from 70 to over 900.

TABLE II

Subject	Stimulus interval in sigma									
	20	80	90	100	115	130	150	200	300	500
Mon	111	302			290			205	220	116
Lon			364		258			361		
Mad		328				349		192		
San	104	144		136		144	144	157	116	103
Ana				203			150	173		
Bos							160	152		
Ste								147		
Asc								187		
Schi								115		
Raz								116		
Fje								243		
Lyo								107		
Rbw								186		
Schu								1022*		
Hir								265		
Harm								69†		
Mel								—‡		

(The table gives the amplitude of the test jerks as a percentage of the normal jerk.)

*This large percentage is due to the small size of the unfacilitated reflex, the relative amount of facilitation being in some cases greater when the unfacilitated reflexes are weak.

†The blow on the knee was uncomfortable for this subject on the second day. This resulted in reduction of the second of each of the paired jerks. The figures for the first day show facilitation.

‡The knee-jerks were absent unless facilitated, hence no percentages are given.

The results have the same trend as those of the main group of subjects but show in addition that the second of two knee-jerks elicited by stimuli 80 sigma apart may show facilitation.

Further Analysis of the Results

The results were further analyzed by computing the facilitation effects separately for each experimental sitting. The average normal jerk for each sitting was compared to the facilitated jerks of that sitting in terms of per cent as described before. Table III shows for the six main subjects the daily averaged percentages of the second of the pairs of jerks, grouping together the results of the 100, 150 and 200 sigma stimulus intervals.

TABLE III

<i>Subject</i>	<i>Experimental sittings</i>			
	<i>First</i>	<i>Second</i>	<i>Third</i>	<i>Fourth</i>
Jac	233	164	161	—
Mac	156	102	89	78
Harr	87	84	83	74
Smi	178	128	210	133
Gol	321	293	336	279
Dur	138	151	172	—
Average	186	154	172	141

It is clear that five of the subjects show a decrease in the facilitating effect or an increase in the inhibitory effect (Harr, Mac) of the preceding stimulus as between the first and the last experimental sitting. In three subjects (Jac, Mac, Harr) this trend continues each day; in two (Smi, Gol) there is an increase on the third day over the second day. One subject (Dur) shows a slight daily increase of facilitation effect.

The results obtained from ten subjects during the experiment in which conditioned responses were developed give collateral evidence of daily changes. Of these there were four cases of decrease of facilitating effect over periods of 5, 3, 3 and 2 days respectively. Two cases show irregular variations over periods of 14 and 10 days. Four cases show increasing facilitation over periods of 14, 3, 3 and 2 days. Subject Schi is an interesting example of facilitation effect being replaced by an inhibitory effect. The daily percentages of normal are 143, 117, 103, 96 and 88.

There are two factors which affect the obtained percentages. One of these is an actual reduction in the facilitating effect of the preceding stimulus; the other is reduction in the amplitude of the unfacilitated jerks from which the daily norms are computed. Especially in the conditioning series

there seems to be a progressive reduction in the amplitude of the unfacilitated kick to the stimulus which has been the second of the pair (The "unconditioned" stimulus). The effect of these two factors is opposed. Whereas the first reduces the obtained percentages, the second increases them.¹⁵ The collateral results, therefore, are not strictly comparable to those obtained with the main group of subjects though they indicate also that the general trend is toward a reduction in the amount of facilitation (or an increase in the inhibition).

Discussion of Results

Three explanations of facilitation of the knee-jerk are common. The inhibitory release theory holds that the facilitating stimulus effects in some way the removal of cerebral or spinal inhibitory influences which otherwise depress the reflex. The tonus theory makes the amplitude of the knee-jerk a direct index of the degree of muscle tonus in the quadriceps group. A third theory explains facilitation by the convergence of afferent impulses at some common point in the central nervous system. The last two explanations are not entirely independent and, taken jointly, are probably most in acceptance by physiologists today.

The explanation in terms of converging afferent paths seems best fitted for the present results. The brief duration of the facilitating effect presents logical difficulties for an explanation in terms of tonus, while it fits in well with a theory which considers it as the result of impulses arriving from the contralateral end-organs (possibly indirectly through higher centers) to summate with the impulses arising on the same side, thus involving a larger number of motor elements in the kick.

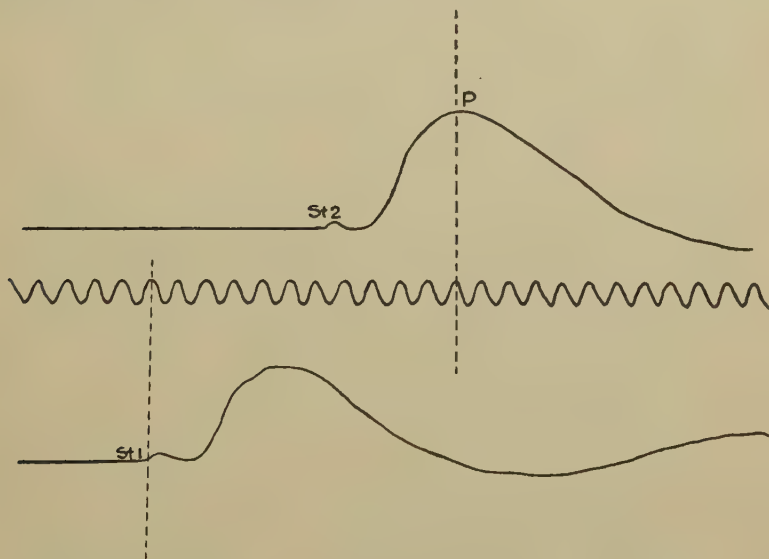
Of main interest to the present investigation is the determination of the time of arrival of the facilitating effect in the records of muscle thickening. How long does it take the effect of blow No. 1 to reach the muscle active in response No. 2?

¹⁵ Interesting in this regard are the results of subject Mon. He was tested for facilitation effects by the same method used with the main group after 14 sittings during which the blow to the left leg had preceded by 1/5 second that to the right 911 times. The facilitating effect of the left stimulus on the right reaction exceeded that of the right stimulus on the left reaction by 57 per cent. The probable cause was the low amplitude of the right reaction when its habitual facilitating stimulus was omitted.

It is clear that this time cannot be directly determined from the results, but must be estimated by interpreting the curves. Since the results are merely exploratory, this estimate must necessarily be rough. The time of arrival of the facilitation effect at the muscle varies over a considerable range as shown by the presence of a point of maximum facilitation (at 150 sigma stimulus interval). In attempting to find the lower limit of this variation four factors must be taken into account:

1. The interval between the two blows.
2. The reflex latency of 30 to 50 sigma.
3. The period during which the discharging center is refractory to stimulation. (This begins as soon as the muscle thickening has passed its highest point.)
4. The period when summation is possible during the recruitment¹⁶ of the reflex. (The recruitment of the knee-jerk takes typically 40 to 50 sigma.)

For a facilitating volley to be effective it must be present before the reflex to be facilitated has passed its crest.¹⁷ This is illustrated by the diagram below.



¹⁶ The term "recruitment" is used by Sherrington to indicate the period of the development of tension in muscular contraction. It is used here to indicate the rising phase of the reflex.

¹⁷ Eccles & Granit (1929), working on the crossed extensor reflex, have shown the effect of facilitating impulses coming before, during and after the recruitment of the reflex.

St. 1 is the blow to the left tendon and St. 2 is the blow to the right tendon coming after an interval. St. 1 sets up afferent impulses which have a facilitating effect on the response to St. 2. In order that these impulses may have this effect, however, they must arrive at the muscle before the reflex contraction has passed its crest at P. A facilitating volley arriving after the crest does not result in addition to the maximum height. P is the *latest* time a facilitating volley can arrive to have an effect. If the interval from St. 1 to P is brief, no facilitation of the second response takes place. This was the case in the present results with a stimulus interval of 40 sigma. The facilitating effect apparently arrives after the crest of the response at this interval.¹⁸

Since at 40 sigma stimulus interval the crest of the second response comes about 120 sigma after St. 1 (stimulus interval of 40 sigma + reflex latency of 40 sigma + recruitment period of 40 sigma,) the latency of facilitation is above 120 sigma for these subjects. However, it cannot be far above it, since with an 80 sigma stimulus interval there was strong facilitation for some subjects. Facilitation of the second response then, begins with a stimulus interval somewhere between 40 and 80 sigma. From this fact the rough estimate is made that *minimum* latency of the facilitation effect was between 130 and 140 sigma for these subjects.

The *typical* arrival time of the facilitation effect may also be estimated. The facilitating impulses from St. 1 will have their greatest effect on the response to St. 2 if they are present during the ascending limb of this response. Taking into account the facts (1) that the maximum facilitation effect was with a stimulus interval of 150 sigma and (2) that with 200 sigma interval the second response was evidently near the limit of the main augmenting impulses, we may estimate that the average time of arrival lay between 150 and 180 sigma for these subjects.

The *upper limit* of the arrival time cannot be estimated without a knowledge of the duration of facilitating impulses. If the response to St. 2 comes after the cessation of the facilitating impulses set up by St. 1, it will not be augmented. But

¹⁸ In occasional instances the arrival of the facilitation effect at the 40 sigma interval is indicated by the presence of secondary thickening of the muscle after the reflex has passed its crest. This was the case with subject Gol.

the duration of the after-discharge cannot be easily determined. It is further probable that more than one level participates in the production of the facilitation, and that *the facilitation at the longer intervals is due to integration at higher levels than the facilitation at the shorter stimulus intervals*. There may be successive volleys of facilitating impulses from progressively higher centers. The presence of a facilitating effect 300 sigma or more after the first stimulus is indicated by the amount of the effect at the 200 sigma interval.

There are no doubt large individual differences both in the average and minimum latency of the facilitation effects. Subject Dur shows a narrow distribution of latencies with a high lower limit. We may also expect some subjects to have a lower limit of latency than that estimated from the results of the present subjects.

The level of origin of the facilitating impulses is a matter of interest. The temporal incidence of the effect indicates that the afferent fibres mediating the facilitating influence do not converge directly upon the discharging center active in the facilitated jerk. However, it is not impossible that the effect takes place on the same level as the knee-jerk center, since it may involve internuncial neurones with relatively slow synapses. Eccles & Granit (1929) report the latency of crossed extensor reflexes in decerebrate preparations to be commonly so low as 40 to 50 sigma, but with weak stimulation this may increase to 500 sigma. That facilitation in "spinal" preparations is possible is well-known. On the other hand, facilitation involving centers as high as the cerebral cortex is shown by the original work of Exner, the well-known results of Lombard (Hoffmann's results strikingly confirm those of Lombard) and those of Graham Brown (1919). Others suggest that spinal centers give the "basic" height of the reflex and that all modifications are cerebral. It is, of course, quite possible that impulses giving rise to facilitation have their origin at more than one level of the neural axis, and that there is a succession of two or more volleys of facilitating impulses, each coming from a different level. There is also the possibility that the reflex contraction of the leg first struck gives rise to further facilitating afferent impulses. Further discussion of the question of level, however, may be most profitably postponed until the results of the conditioning series and voluntary reaction series have been presented.

Factors Causing Depression

All reductions of the knee-jerk need not be explained by a single principle. It seems not unreasonable that two or more influences are responsible for the reductions in amplitude observed in these results.

The post-facilitation depression, as found especially in subject Dur, may be explicable in terms of some type of fatigue process. The phenomenon known as the "relatively refractory period" suggests a ready analogy.¹⁹ The facilitating impulses may leave the knee-jerk center relatively inexcitable after their arrival. An alternative explanation is that the first stimulus gives rise to both facilitating and inhibitory impulses and that the facilitation effect is stronger while it lasts but has a shorter duration than the inhibitory effect. The inhibitory effect then shows up after the facilitation effect is gone.

In the case of subjects Harr, Mac, Harm and Schi the stimulus to one tendon was observed to have a distinct inhibitory effect on the subsequent response of the other leg during one or more of the sittings. In other subjects there appeared a marked reduction in the facilitating effect of the stimulus when the subject served over several experimental periods. The two phenomena may well be treated together, since facilitation was found to grade into inhibition. It is interesting to notice that the results do not suggest that the time of arrival of the inhibitory effect differs from that of the facilitation effect but that its duration is probably greater. In the case of subject Harr the effect began at 100 sigma stimulus interval and then showed a slight increase at each interval thereafter.

There are three possible explanations of this inhibitory effect. (1) It is a frequent clinical observation (Böhme, 1927) that painful stimulation may inhibit the knee-jerk. An instance of this is the second sitting of subject Harm to whom the blow at that time was slightly painful. When the normal jerk at that sitting was compared to the jerk preceded by a blow on the contralateral painful tendon, the latter was but 27 per cent of the normal. It is significant that the discomfort did not affect the amplitude of the knee-jerk of the leg with the painful ten-

¹⁹ The relatively refractory phase of the knee-jerk is of long duration. Dodge (1927) reports it up to $\frac{1}{2}$ second and above, while Strughold (1926, 1928) reports it as lasting from 3 to 10 seconds.

don, but only a knee-jerk following it after an interval.²⁰ All other subjects denied that the blow was painful. (2) The slight discomfort incidental to the body jar from the blow and to the swing and fall of the leg during the reflex may have directly (by a mechanism at some point in the facilitating arc similar to reflex reversal in the reflex arc), or indirectly (by learning or conditioning) given rise to inhibitory impulses.²¹ (3) The blow to the tendon may set up both facilitatory and inhibitory impulses. In some subjects the facilitatory impulses may be relatively weaker than the inhibitory impulses.

In the foregoing explanations there is the possibility that the inhibition has no other reflex accompaniment, or that it is allied in a reciprocal relationship with flexor contraction of the inhibited leg. Whereas Dodge (1911) noted that the voluntary contraction of the leg flexors increases the knee-jerk, Sherrington (1906) found that reflex contraction of the flexors inhibited a concurrent knee-jerk.

As explanations of the decrease of facilitation effects in the later sittings, the following suggest themselves. (1) As noted above, the discomfort of the repeated jerks of the leg may lead to a type of negative conditioning so that extensor inhibition results (either alone or allied with flexor contraction). (2) Adaptation to the experimental situation may reduce attention to the knee-jerks. It may be that attention is a favorable condition for facilitation. (3) Adaptation to the situation may reduce tenseness. This reduction in tenseness may, by removal of facilitating influences, lead in turn to a reduction in the excitability of the arc by which facilitation is mediated. (4) The process known as "negative adaptation" may hold also for the facilitatory process.

All the above factors may play a part in the production of the results. However, that an active depressant agent is at work (extensor inhibition) is indicated by the fact that the second jerk of the pair, at first facilitated, not only loses this

²⁰ Although the amplitude of the homolateral reflex was apparently unchanged by the condition which led to inhibition of a subsequent response of the other side, there was some evidence that it was also affected. The responses seemed somewhat more twitch-like, the relaxation of the muscle being more rapid.

²¹ The majority of physiologists regard inhibition as an active process comparable to excitation. Its locus of action is central (probably at the final motoneurone, see Fulton (1926), its action by stoppage of impulses in the motor nerve. Howell (1925) regards it as being mediated in all cases by specific inhibitory nerves.

effect but later becomes depressed as compared to the normal jerks for the same day. It is not improbable that the two processes of facilitation and inhibition are concurrently present, the latter finally obscuring the former. Taken in conjunction with the results of the conditioning series, the best explanation of the facts seems to be that facilitation does show negative adaptation, and that, in the case of some subjects, an active inhibitory process may develop. If both are concurrently present, the resulting amplitude of the knee-jerk is probably determined by algebraic summation (Sherrington, 1910) of the two effects.

Significance of Results

The presence of strong facilitation having its effect 120 to 300 sigma after the stimulus indicates the presence of an integration of stimulus and contralateral response which we may expect will be the basis for the development of conditioned responses. The latency of conditioned responses should fall within these time-limits.

The presence in some subjects of an inhibitory effect is of obvious significance for conditioning. We should not expect such subjects to develop readily a conditioned knee-jerk.

Conclusions

A blow on the patellar tendon of one leg augmented a subsequent knee-jerk of the other leg. The facilitating impulses affected the muscle group involved in the augmented jerk at an estimated minimum time of 130 to 140 sigma after the incidence of the first blow. The typical latency was estimated at 150 to 180 sigma while their duration may extend until 300 sigma or more after the stimulus.

Under the conditions of this experiment the facilitation effect showed a daily decrease over a period of days in most subjects.

A preceding contralateral blow may have an inhibitory effect on the knee-jerk of some subjects.

Individual differences are marked.

SECTION V. CONDITIONED RESPONSES

Conditioning of the contraction of the quadriceps muscle has been proved possible. The first observations were made by Twitmyer (1902). During a study of facilitation effects, he noticed that in some subjects the accidental omission of the blow to the leg was followed by an involuntary kick. He developed such conditioned responses to the sound of a bell in five subjects. A second early study was that of Shevaleyev in Bekhterev's laboratory. Using the Sommer apparatus, screened from the subject, conditioned responses of the leg to a bell were developed in each of the seven female subjects after 8, 10, 21, 56, 65, 70 and 78 combinations. The stability in terms of successive appearances without reinforcement varied from 2 to 8. No measures of response-time were taken. Differentiation of the bell from another bell was successful in one of four subjects.²² Dodge (1911) noted the presence of "involuntary anticipatory contractions" as being the basis of some of the most pronounced inhibitions appearing in knee-jerk records. He stated that this might occur even in direct opposition to conscious effort to prevent it. Cornil & Goldenfoun (1928) applied the conditioned knee-jerk as a clinical method for use with children. They reported four cases in two of whom leg response was conditioned to the sound of a tuning-fork with the aid of a facilitating stimulus in the form of a *blow on the other knee*. Switzer (1930) reported the development in two of five subjects of "backward" conditioned responses to a bell sound. Schlosberg (1928) has reported the most ambitious study of conditioned leg reactions. His problem was the study of the effect of various factors on the rate of formation of the conditioned response and the study of its stability. A gravity percussion hammer gave the stimulus, and responses were recorded by muscle thickening. Conditioned responses were developed in 44 of 49 subjects. Responses were conditioned to a bell, click, buzzer, and tactual pressure. Great individual variations both in frequency and amplitude of conditioned responses were found. Instability was the rule, even during one experimental sitting. Variation of the stimulus in-

²² I am indebted to H. S. Razran for an abstract of this publication.

terval between 0.20 and 0.44 second had no significant effect on the ease of formation. An interval below 0.11 second increased the difficulty of conditioning. The most important single factor affecting the speed of conditioning was found to be the use of facilitation in the form of voluntary reaction accompanying the kick. This more than doubled the frequency of conditioned responses. The conditioned response of the leg was found to differ from the reflex response chiefly in its greatly diminished steepness of initial rise and in its longer reaction-time. Average reaction-times of four subjects were 0.47, 0.40, 0.34 and 0.28 second respectively, while the lowest times recorded in each case were 0.47, 0.40, 0.20 and 0.16 second. Voluntary kicks of the leg were found to have similar contraction-curves and reaction-times.

Dodge (1927) reported negative results from the use of a stimulus situation very similar to the one used in the present investigation. An effort was made to produce crossed reflexes by simultaneously stimulating the two knee-jerks. "In spite of hundreds of cases of simultaneous stimulations true crossed reflexes were never elicited. Similarly, simultaneous stimulation of the right and left final common paths to the quadriceps by voluntary effort and by normal reflex stimulation, respectively, also failed to produce a reconfiguration of the mechanism of the knee-jerk." pp. 68-69.²³ In another experimental series two knee-jerks were elicited from the same leg at an interval of $\frac{1}{2}$ second. In spite of hundreds of repetitions the second stimulus was never anticipated.

The stimulus situation used by Dodge and the stimulus situation used in the present investigation have the advantage of offering several theoretically possible levels of integration, since both stimuli enter the neural axis at the lumbar level. To past reports of conditioning of the knee-jerk it adds (1) the taking of high-speed records throughout the conditioning trials so that a genetic study of the development of the response and an accurate determination of the latency and form of the reaction can be made, and (2) the registration of an identically comparable response to both the conditioned and the unconditioned stimulus. The registration of the original

²³ At the time the present research was prosecuted the writer was not acquainted with this work done by Dodge.

response to the conditioned stimulus has important theoretical implications as recently pointed out by Razran (1930).²⁴

Procedure

Because the purpose of the investigation was analytical rather than the establishment of norms, the procedure of experimentation was varied. The subjects served for different periods of time (from one to twenty experimental sittings) and the details of procedure varied. The general plan of experimentation, however, was the same for most of the subjects (the first eleven subjects in Table IV on page 36). There were (1) a period during which the stimulus for each knee-jerk was presented singly for the establishment of norms of response and for adaptation on the part of the subject, (2) a period during which double stimulations were given to develop conditioned responses and during which tests of response to single blows were made, (3) a period during which single stimuli were again presented to trace the behavior of the responses during "experimental extinction." For details of the number of stimulations given in each period Table IV should be consulted. Column 1 shows that of this group of subjects (the first eleven in the table) four served for 13 to 20 days, four served for 4 days, one for 6 days and two for but 1 sitting. Column 3 shows that the number of stimulations of each leg singly was from 60 to 300 in the four subjects who were to serve for the longer period and about 20 for the others. Column 2 shows the number of sittings during which these stimulations were given. Columns 5 and 6 show the same data for the double stimulations given to develop conditioned responses. The number of double stimulations ranged from 17 to 911, the sittings necessary to give them from 1 to 15. Columns 7 and 8 give the same data for the extinction period. The number of single stimulations in this period was as high as 404, the sittings during which they were given as many as 5. Columns 9 and 10 show respectively: (9) voluntary reactions made after the completion of the preceding three periods, and (10) retests for the conditioned response after the voluntary responses. The results of the voluntary reactions will be presented in the next section.

²⁴ See also Borovski (1929), Erofeeva (1912), Ukhtomski (1911).

TABLE IV

Subject	Single st. to establish norms			Double st. for conditioning		Extinction period		Voluntary reactions after conditioning	Conditioning after voluntary reactions
	Total no. of experimental sittings	No. of experimental sittings	No. of stimuli	Voluntary reactions before conditioning	No. of experimental sittings	No. of stimuli	No. of experimental sittings	No. of stimuli	
Hir	20	2	106	—	14	871	5	404	84
Mon	19	3	300	—	15	911	1	104	37
San	15	2	114	—	11	643	1	100	119
Rbw	13	2	60	—	10	478	—	—	36
Ste	4	1	20	—	4	186	1	40	89
Lyo	4	1	22	—	4	202	1	16	70
Fje	4	1	20	—	4	191	1	12	83
Harm	4	1	20	—	4	184	2	45	65
Raw	1	1	6	—	1	17	—	*	—
Schi	6	1	20	—	5	326	—	—	47
Raz	1	1	30	—	1	50	—	—	—
Schu	4	1	20	80	3	135	1	10	80
Asc	4	1	20	79	3	144	1	22	84
Mad	3	1	20	67	1	14	—	—	90
Lon	2	1	20	72	1	15	—	—	—
Dur	1	4†	75	79	1	13	—	—	—

*The services of this subject could not be obtained for further experimentation.

†Extinction period omitted since no conditioned responses had been recorded.

‡The norms were gotten during previous sittings in the facilitation experiment.

In the case of the last five subjects in the table voluntary reactions were made before the beginning of the conditioning period. The procedure otherwise was the same. Automatic kicks of the leg on contralateral stimulation in these cases should probably be classed under the category of *habit* rather than that of *conditioned response*.

The general method of experimentation was as described in Section III, especial care being taken to eliminate secondary sound cues. The importance of attention to the reading matter was particularly stressed in the instructions to the subject. Although Schlosberg found that the use of facilitation in the form of voluntary activity was a great aid in the development of conditioned responses, this method was rejected because of the added difficulty of interpretation of results so obtained. It may be that automatic leg reactions gotten by the use of facilitation of this kind have their origin in the discharge of impulses set up by the voluntary activity rather than those set up by the conditioned stimulus. They might therefore show a closer correspondence to voluntary action than would be the case when the subject's attention is entirely distracted from the conditioning stimulus. Schlosberg notes that voluntary action in this case may act either as a facilitating factor or as an additional unit in the constellation of stimuli.

As stated above, the general plan of experimentation provided for (1) an adaptation period, (2) a conditioning period and (3) an extinction period. In both the adaptation and the extinction periods the stimuli to the right and left leg were given an equal number of times in random order at intervals of $\frac{1}{2}$ minute. In the conditioning period one stimulus preceded the one to the other leg by $\frac{1}{5}$ second. Double stimulations were given at $\frac{1}{2}$, 1 and $1\frac{1}{2}$ minute intervals during an experimental sitting of one hour. There were in each sitting 40 of the $\frac{1}{2}$ minute, 24 of the 1 minute, and 10 of the $1\frac{1}{2}$ minute intervals distributed in a random order. Exactitude of interval was avoided to reduce anticipation effects, a variation of five seconds in either direction being frequently introduced in the $\frac{1}{2}$ minute intervals. The typical experimental sitting consisted of 69 double stimulations, 3 stimulations of the left leg alone, and 3 of the right leg alone. The single stimulations usually occupied the numerical positions in the series of

20, 25, 45, 50, 70 and 75. The number of single stimulations was increased if conditioning seemed fairly stable.

The use of the relatively long intervals between double stimulations was adopted to avoid a possible facilitation effect carrying over from the preceding stimulation. Graham Brown (1915) has shown that a second stimulus following at so much as 20 seconds may show heightened reaction. In dealing with skeletal muscle reactions an interval of $\frac{1}{2}$ minute is probably sufficient to avoid such a period of raised excitability. That the intervals were long enough is shown by computations from the results of subject Mon. In the table below, derived from the averages of 1670 knee-jerks during the conditioning period, are given the average amplitudes of the records of muscle thickening after each interval. It is seen that the first knee-jerk of the pair shows no influence of the interval, while the second shows a slight tendency to increased activity at the

<i>Interval</i>	<i>First k-j of Pair</i>	<i>Second k-j of Pair</i>
$\frac{1}{2}$ minute	3.447 mm.	4.549 mm.
1 minute	3.558 mm.	4.665 mm.
$1\frac{1}{2}$ minute	3.432 mm.	5.056 mm.

longer intervals. This latter may be due to the wearing-off of a fatigue process in the facilitating arc or (more probably) to complex factors of expectation at the longer intervals.

The use of single stimuli to both the right and left leg in the conditioning period was for the purpose (1) in the case of the single presentations of the "conditioned" stimulus to test for conditioned responses and (2) in the case of the presentation of the "unconditioned" stimulus to test for backward effects or for "generalization." Since the two stimuli are at homologous points, we may expect (from the results of animal conditioning)²⁵ that a response conditioned to one of them would also be made to the other (commonly referred to as "generalization"). The nature of the response would then determine whether it should be called a "backward" response or ascribed to generalization.²⁶

The $\frac{1}{5}$ second stimulus interval was decided upon after

²⁵ See Anrep (1923).

²⁶ The physiological terms used by Pavlov and others to describe the phenomena of conditioning are not entirely satisfactory for the description of the present results. Their use here does not imply acceptance of the Pavlovian theories.

preliminary experimentation. It falls within the limits of the facilitating effect from the contralateral stimulus. It makes possible the detection of conditioned responses even during the double stimulations, when the muscle begins to contract before the blow strikes. Schlosberg found the interval to be favorable for conditioning, while shorter intervals were unfavorable. Further justification of its use will appear from the results.

In order to test for the possible presence of conditioning to secondary sound cues penetrating the sound-screen, these cues were given without accompanying leg stimulation. By closing both release magnet circuits at the throw switches (see Section III) the percussion hammers were not released while the timing pendulum and kymograph were in action. Leg reaction to these noises would then show that conditioning to sound cues was present. These tests were made more rigid by selecting periods of lull in the street noises (which were intense) for their presentation.

Results

The results obtained are notable above all for the complexity of the phenomena and for the differences between subjects. Because of the individual differences, no completely adequate conception of the results is possible without a separate analysis of the results of each subject. The differences between subjects, however, do not seem to be differences in the essentials, for certain phenomena are general in their appearance. In the presentation of these phenomena the purposes of exposition are best served by selecting for detailed analysis one subject in whose case the results are most varied and complete. The results of other subjects will then be inspected for verification and additions. Because of the character of the results, this analysis has been made largely qualitative.

Results of Subject Hir

The subject selected for this analysis is Hir, number 1 in Table IV. He was obtained through the University Appointments Office and was paid for his time. He was 21 years old, a junior in the pre-medical course, a member of the crew and a swimming instructor. He exhibited no knowledge of conditioning and throughout the experiment had no conception of its purpose. He served for 20 experimental sittings of which

the first 2 were a period of adaptation and for establishment of norms of response, the next 13 the conditioning period, the next 4 a period during which extinction was attempted, and the last devoted to the recording of voluntary reactions.

The first sitting was brief, being taken up by the determination of the apparatus settings to be used throughout the experiment. A few responses of each leg were recorded. The second sitting was the main adaptation period. 100 stimulations (50 of each leg) were given at intervals of $\frac{1}{2}$ minute. The knee-jerks were active, normal in shape, with an average latency of 35 sigma. No crossed reflexes were recorded.

In the third to fifteenth sitting the blow to the left leg preceded that to the right leg 871 times. The stimulus interval was about 208 sigma.²⁷ The blow to the left leg alone was given 71 times, that to the right leg 55 times. The daily frequency of these tests was greatest during the later sittings.

It is well to sketch the main results briefly before describing them in detail. It was found that combined stimulation gave rise to two kinds of conditioned responses which were clearly different. They were distinguished from one another by speed of development, latency, characteristics of the contraction and by their behavior on discontinuance of double stimulations.

The one kind of conditioned response first occurred after two double stimulations. It was a response of short latency (120 to 180 sigma) and occurred originally as a bilateral response. Stimulation of one tendon caused, in addition to the fast reflex-knee-jerk, a simultaneous contraction in both quadriceps. With repetition of the double stimulations these bilateral responses first increased in frequency, then decreased. However, it was only as a bilateral response that it decreased, for a secondary response of the leg stimulated continued to be made when the simultaneous crossed contraction had largely disappeared. This secondary response did not disappear during attempted experimental extinction.

The second kind of response developed only after 316 double stimulations. It was distinguished from the other type of conditioned response by its longer latency (200 to 300 sigma) and by the fact that it was not bilateral, occurring as a re-

²⁷ This interval was used throughout. Due to slight variations in setting the break contacts, this interval varied a few sigma in either direction.

sponse of only that leg which during conditioning received the second of the two blows. It disappeared quickly when double stimulations were discontinued.

In the succeeding description the first kind of conditioned response is referred to as the "short-latency response." The second kind is referred to as the "long-latency response."

The conditioning procedure resulted in a marked decrease in the amplitude of the fast reflex knee-jerk.

Short-Latency Conditioned Responses

The first two double stimulations at the first sitting of the conditioning period showed marked augmentation of the response of the right leg due to the preceding blow on the left. (Plate I on page 15 shows facilitated knee-jerks of this subject.) At the third double stimulation the first conditioned response was given. There was marked pre-stimulation thickening of the right quadriceps. The characteristics of this response (see Plate II, cut 1, for a similar response) were as follows:

1. Its latency figured from the contralateral blow on the left tendon was 132 sigma.

2. Its amplitude was that of an active normal knee-jerk (109% of the average normal of the adaptation period).

3. Its steepness of rise was close to that of the normal reflex. Its recruitment time (measured from the point of the first muscle thickening to the point where it attained 9/10 of its final height) was 60 sigma as compared to 40 sigma for a reflex jerk of equal size.

4. The response was *bilateral*. A further thickening of the left quadriceps, added to the reflex contraction already present, coincided with the beginning of the contraction of the right muscle group.

5. The duration of the crossed response could not be determined, since it was complicated by the blow on the tendon (showing as a sharp knob just after the crest of the contraction). No further rise resulted from the tendon stimulus.

Responses showing the above characteristics occurred also on the 22nd and 28th stimulations of this day. During the remainder of the day's sitting, conditioned responses were given neither during the double stimulations nor during the tests.

During the second experimental sitting of the conditioning period prestimulation contraction of the right quadriceps occurred six times. The average amplitude of these reactions was less than that of the normal reflex. Evidence of the bilaterality of the response was clear in but one of the cases. However, under vigorous reflex contraction of the left muscle group, the discharge on this side may either have no effect, or may be masked by existent muscle thickening. (See Plate II, cut 3.)

In the same sitting it was shown that the response might in some cases be unilateral, lacking the crossed component. A distinct secondary rise, added to the reflex contraction of the left leg, occurred in two cases without an accompanying prestimulation contraction of the right quadriceps. (See Plate III, cut 1.) This response was in one instance of sufficient amplitude to dwarf by comparison a relatively weak reflex contraction already present. (See Plate III, cut 3.)

At the 50th stimulation of the same sitting, the blow to the *right* leg was presented alone and was followed by a bilateral response with all the characteristics described above in the case of bilateral responses to the left blow. (See Plate II, cut 2.) This response to the "unconditioned" stimulus could be regarded as an instance of so-called "generalization."²⁸

Such bilateral responses continued to appear throughout the 13 sittings of the conditioning period. They occurred to stimulation of either the left or the right leg. Seventy per cent of them fell between 130 and 170 sigma after the stimulus. They reached their greatest frequency during the third sitting of the conditioning period, appearing ten times in the hour. From that sitting, however, they showed a decrease in frequency until during the seventh sitting, and thereafter until the thirteenth they did not occur more than twice during a sitting.

Along with this decrease of the bilateral responses there occurred an increase in the number of unilateral secondary contractions of the muscle stimulated (as in Plate III). These, as noted above, were evidently the same phenomenon as the bilateral responses, but the crossed component did not result in contraction. However, that a contralateral (crossed) com-

²⁸ The generalization in this case probably rests on functional connections already present in the central nervous system. It is therefore not identical with the phenomenon present in the early stages of conditioning as described by the Russian physiologists.

Per Cent of Total No. of Stimulations

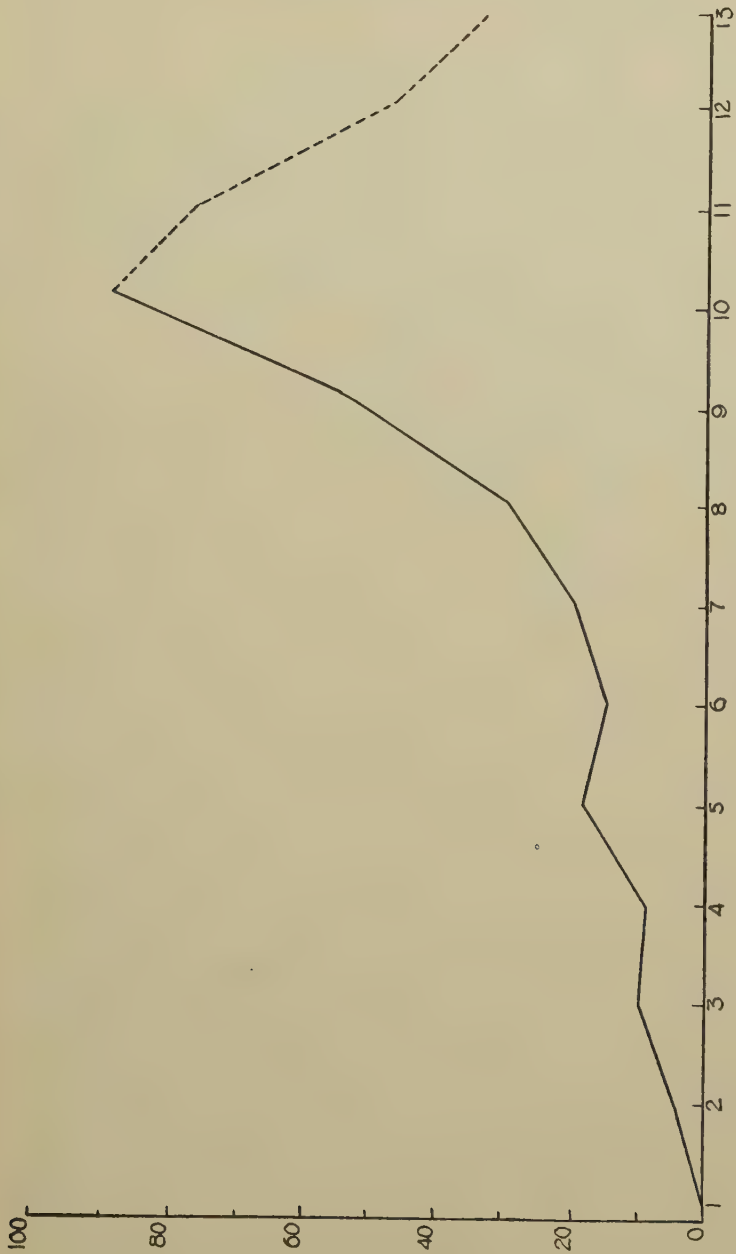


FIGURE II. DAILY FREQUENCY OF UNILATERAL SECONDARY CONTRACTIONS (SUBJECT HIR).
After the Tenth Sitting the Procedure and Conditions Were Somewhat Altered.

ponent was present was indicated by the continuance throughout the conditioning period of marked facilitation of the reflex response of that side.

Figure II shows the occurrence of these unilateral secondary contractions in per cent of the total number of stimulations. The curve shows that their frequency continued to increase until the tenth sitting of the conditioning period.²⁹ At that time these responses were clearly present in 89% of the stimulations. At the eleventh sitting there was a decrease of such responses and a further decrease occurred in the twelfth and thirteenth sitting. However, it is not certain that this decrease represents a true tendency. The eleventh sitting was on the afternoon of the same day as the tenth. The subject was available for only five days more so that two sittings were necessary each day to complete the results. The decrease may have been due to the less favorable time of the day (mid-afternoon heat as compared to the cool weather of the morning) or to fatigue. During the twelfth sitting, the stimulus interval was shortened to 140 sigma and the thirteenth sitting occurred on the afternoon of the same day. In view of this variation of conditions, no conclusion as to the reason for the decrease in frequency of this response is possible.

The decrease of the stimulus interval to 140 sigma during the twelfth sitting apparently resulted in an increase in the number of bilateral responses during the next sitting when the stimulus interval was again increased to 1/5 second. Several such responses occurred during the first part of the hour.

At the end of the thirteenth sitting, the subject's ability to inhibit this response was tested. He was told that, as usual, there would be two blows. He was asked to prevent response to either of the blows. The arrival of the stimuli was to be signalled to him one second before they were given. No method of inhibition was suggested. The immediate result of these instructions was a marked increase in the amplitude of the reflex response to the blows and a recurrence of the bilateral responses showing as pre-stimulation contraction of the right quadriceps. After ten attempts at inhibition the subject apparently achieved some degree of success, for the secondary responses disappeared and the reflexes were reduced. It is

²⁹ The positive acceleration of the curve would be expected, since the response was not present at the beginning.

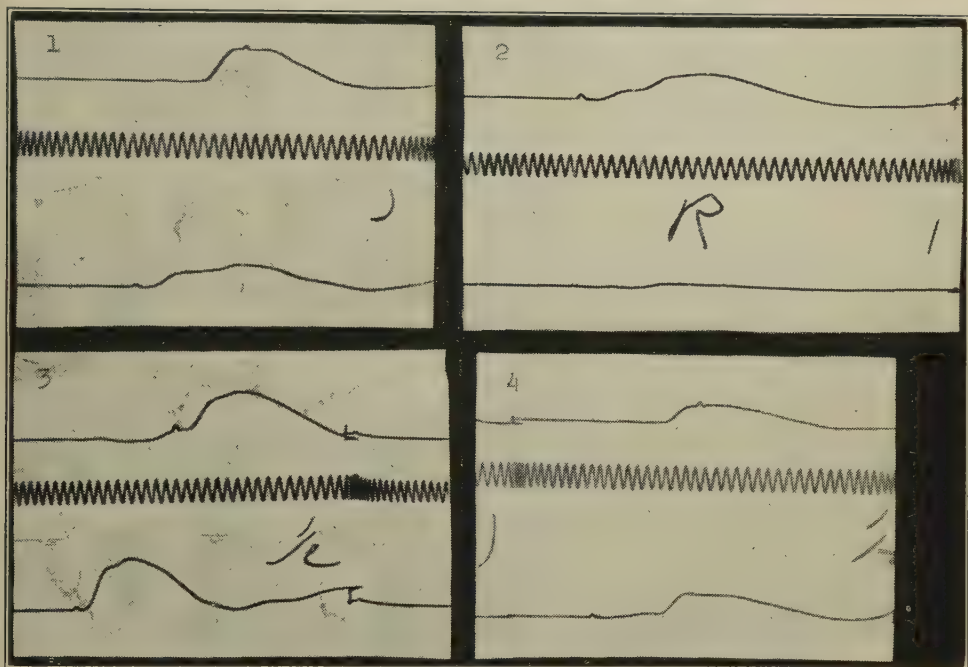


PLATE II. BILATERAL RESPONSES OF SUBJECT HIR.

The lower line in each is the left quadriceps, the upper line is the right quadriceps.

Cut 1. Bilateral response during double stimulation. The right blow fell just as the contraction of the right leg reached its crest.

Cut 2. Bilateral response to right stimulus alone. In this case the crossed contraction is weak.

Cut 3. Bilateral response during double stimulations. The homolateral component is masked by the active reflex contraction of the left quadriceps. The right stimulus falls in the rising phase of the crossed component and gets a reflex response.

Cut 4. Bilateral response during double stimulations. The reflex response to the left blow is slight.

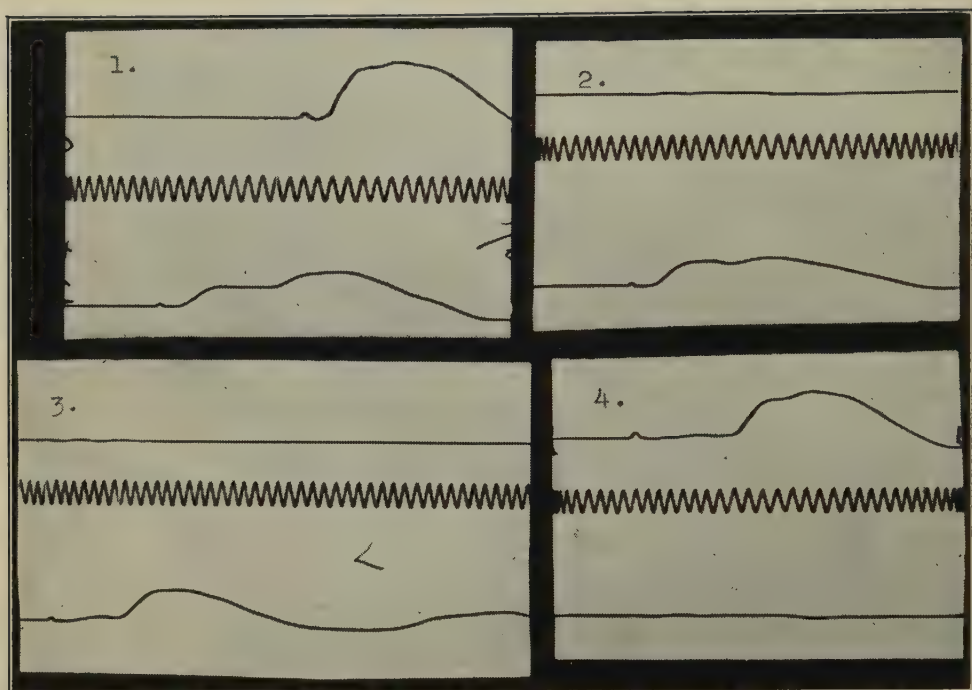


PLATE III. UNILATERAL SECONDARY CONTRACTIONS OF SUBJECT HIR.

Cut 1. Strong secondary contraction during double stimulation. Moderate reflex response already present.

Cut 2. Strong secondary contraction of left quadriceps with moderate reflex contraction. Right stimulus omitted.

Cut 3. Strong secondary contraction with weak reflex contraction.

Cut 4. Strong secondary contraction with reflex contraction almost absent.

suspected, however, that this was because the subject had given up the attempt.

A full description of the short-latency conditioned response shows it to have the following characteristics. (See Plates II and III.)

1. It appears on stimulation of either the left or right (first or second) leg. No difference in relative frequency of response to either stimulus can be seen throughout the series.

2. It has a typical latency of 135 to 165 sigma, though it seems to go, rarely, as low as 100 sigma and as high as 190 sigma. 120 and 180 sigma represents its normal range.

Figure III shows the distribution of times of the unilateral responses. Taking into account all such responses recorded during both the conditioning and extinction period, there was a total of 524 clear instances of secondary contraction in the records of this subject. Three hundred and twenty-two of the more definite ones were measured for latency. These 322 make up the distribution in Figure III. The skewness of the distribution is a natural consequence of the fact that the response takes place on a reflex background. The responses of lower latency are relatively infrequent either because they fall in a refractory period just after the crest of the jerk, or because they are masked by existent contraction. The center of the distribution is probably also misplaced due to the difficulty of measuring the latency of a response taking place on a background of contraction. It is not always easy to determine the exact point where the muscle begins to thicken in secondary contraction. This becomes especially important when the reflex primary contraction is strong. The obtained median value of these responses (160 sigma) for this reason and because of the absence of the lower end of the distribution is probably 10 sigma or more above the true median of the beginning of the response.³⁰

3. It is a bilateral response. With continued double stimulation with a stimulus interval of $1/5$ second it becomes unilateral, the crossed component failing to arouse active contraction.

³⁰ Throughout the present study the median has been used as a measure of central tendency for latencies of response. In those cases where measurements are few it seems a more *characteristic* measure than the mean. Average values would in most cases be slightly higher.

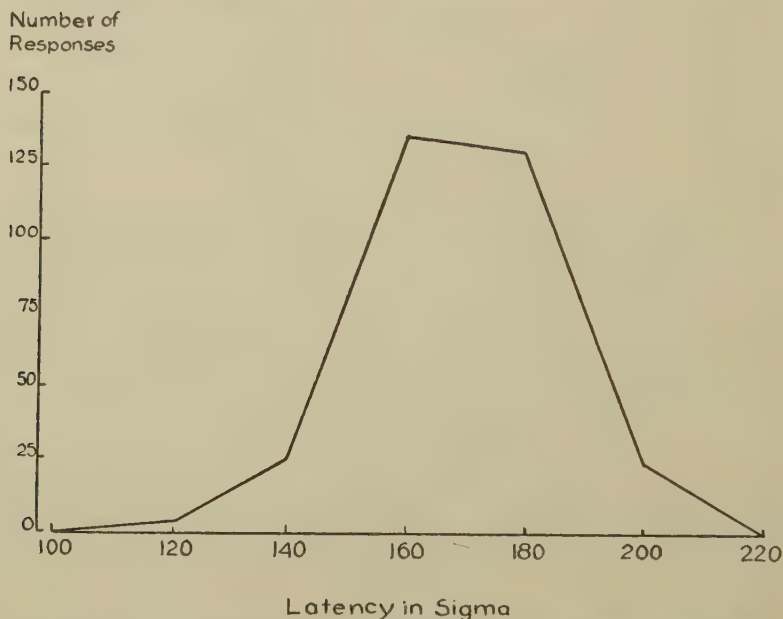


FIGURE III. DISTRIBUTION OF LATENCIES OF UNILATERAL SECONDARY CONTRACTIONS (SUBJECT HIR).

4. It shows at best somewhat slower recruitment than the reflex response. The recruitment period is variable and may be considerably lengthened in cases of slight contraction.

5. The amplitude of the response may be as great as that of the normal reflex. As in the case of the reflex response, it shows great variability. The crossed component in bilateral responses becomes smaller with successive sittings; while the homolateral secondary contraction shows, on the whole, an increase in amplitude.

6. In those cases where it is bilateral it behaves toward intercurrent stimulation as do other muscle contractions. A stimulus falling during its rising phase results in summation (see Plate II, cut 3), while a stimulus at or beyond the crest elicits little further response (see Plate II, cuts 1 and 4). A stimulus, falling shortly before its beginning, may be assumed to give rise to summation of the crossed component with the reflex response (*i.e.*, facilitation).

7. The contraction-curve of the response (see Plate III, cuts 3 and 4) is not unlike that of the reflex. As noted above, however, its recruitment is slightly slower. Its duration varies with the recruitment speed so that the weaker responses have little similarity to the reflex jerk.

8. The response may occur in the presence of slight reflex contraction (Plate II, cut 4 and Plate III, cuts 1 and 4). There are many cases of secondary contraction where the primary reflex contraction measured less than $\frac{1}{2}$ millimeter. There are, however, many cases of slight reflex contraction with no considerable secondary contraction and, on the other hand, of active reflex contraction with relatively strong secondary contraction.

9. The response can occur in spite of the subject's desire to prevent leg movement.

The further behavior of this response under attempted "experimental extinction" will be described after discussing the second type of response which developed during the conditioning period.

Long-Latency Conditioned Responses

During the fifth sitting of the conditioning period a new type of response first appeared. When the blow to the left leg (the conditioned stimulus) was presented alone, it was followed after an interval of 280 sigma by active contraction of the right quadriceps. All of the bilateral responses recorded previous to this had a latency of 185 sigma or less. That the long-latency kick was a different response was shown in the succeeding sittings where it occurred with increasing frequency in tests of the responses to the left blow alone.³¹ There was also evidence that the discharge giving rise to this long-latency response was present during the double stimulations. It then showed as a secondary contraction of the right quadriceps,³² and in some cases as a pre-stimulation thickening of the

³¹ Since the stimulus interval was 208 sigma, contraction of the right quadriceps at latencies exceeding this would be visible only if they came just as the blow fell. The reflex to the blow covers responses coming later. The practical limits of identification of the conditioned responses during double stimulations falls at about 215 sigma.

³² Such secondary contraction of the right quadriceps had not been present during any of the *double* stimulations in the first four sittings. The secondary contractions noted before had occurred only when the right blow was given alone. It is, however, probable that not all of the secondary contractions of the right quadriceps during the double stimulations were due to the long-latency discharge initiated by the stimulus to the left, but that some of them were the same phenomenon which occurred in the shorter-latency responses. This might happen under circumstances where the recovery of the mechanism functional in the short-latency secondary contraction was practically complete before the blow to the right tendon fell.

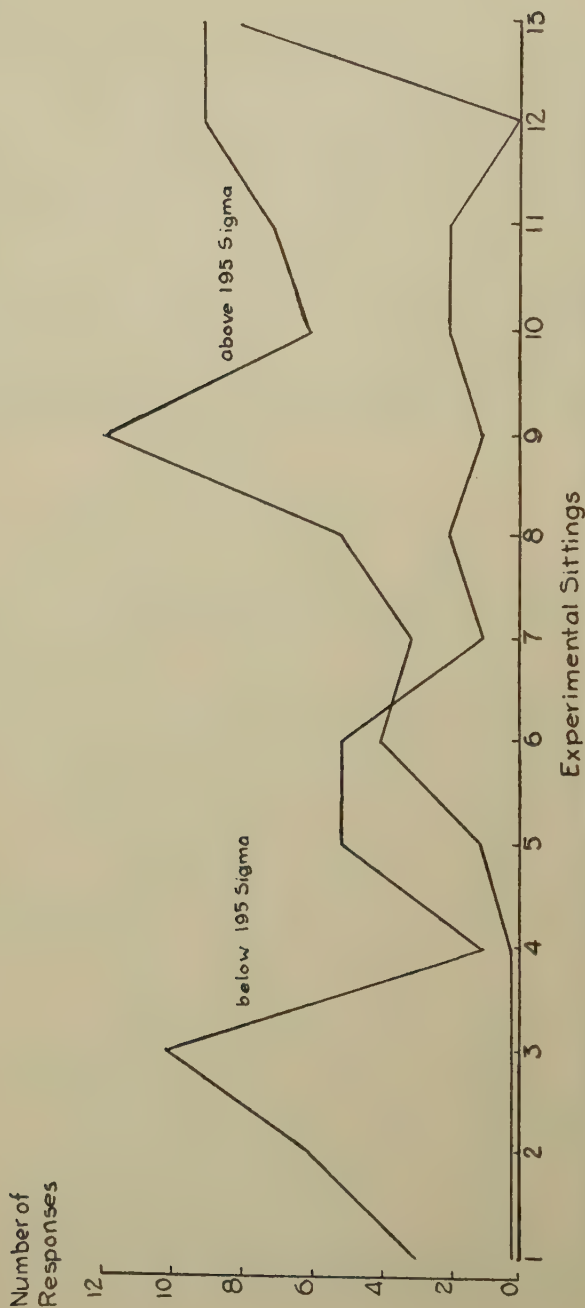


FIGURE IV. FREQUENCY OF CASES OF CROSSED CONTRACTION OF SHORT AND LONG LATENCY (SUBJECT HIR). The curves show that the short-latency bilateral responses became fewer in the later sittings, while the long-latency responses increased in frequency. (The rise in the number of short-latency contractions at the thirteenth sitting is due to changed procedure.)

muscle very close to the incidence of the blow. Further evidence of its presence was an increase throughout the conditioning period in the amplitude of the contraction of the right muscle when facilitated by preceding stimulation.

Figure IV shows the development of these long-latency reactions of the right leg over the thirteen sittings. It also shows the frequency of the bilateral responses of shorter latency. A part of the variability in the curve of responses with latencies of 195 sigma and above is due to the varying number of presentations of the left stimulus alone in the different sittings.

Beginning with the sixth sitting, these responses were fairly regular. Figure V shows the percentage of tests (left blow alone) in which contractions of the right quadriceps occurred. It is seen that, in the later sittings, conditioned responses were regularly present in the tests. These responses were of long-latency. The responses made during the tests were of the shorter-latency bilateral type only during the third sitting.

Figure VI further illustrates the difference between the long-latency and short-latency responses. The lower curve represents the distribution of latencies of contractions of the right quadriceps during the tests where the left blow was given alone. The distribution of the long-latency responses is from 185 to 305 sigma with a median value of 255 sigma. The short-latency responses fall much lower in the time scale so that there is a clear bimodal distribution with no overlap. The upper curve shows the presence of the long-latency responses during double stimulations, showing here as pre-stimulation contraction just as the blow fell. The curve is made up of *all* cases where the right quadriceps was observed to begin contraction, either before it was stimulated, or just as the blow fell. It is probable that this curve is the summation of two distributions which overlap but little. The high point close to the incidence of the second blow is very likely the lower part of the distribution of long-latency responses.

Records of such long-latency responses are given in Plate IV. The characteristics of this type of response are as follows:

1. Its median latency is 100 sigma greater than that of the previously described responses.

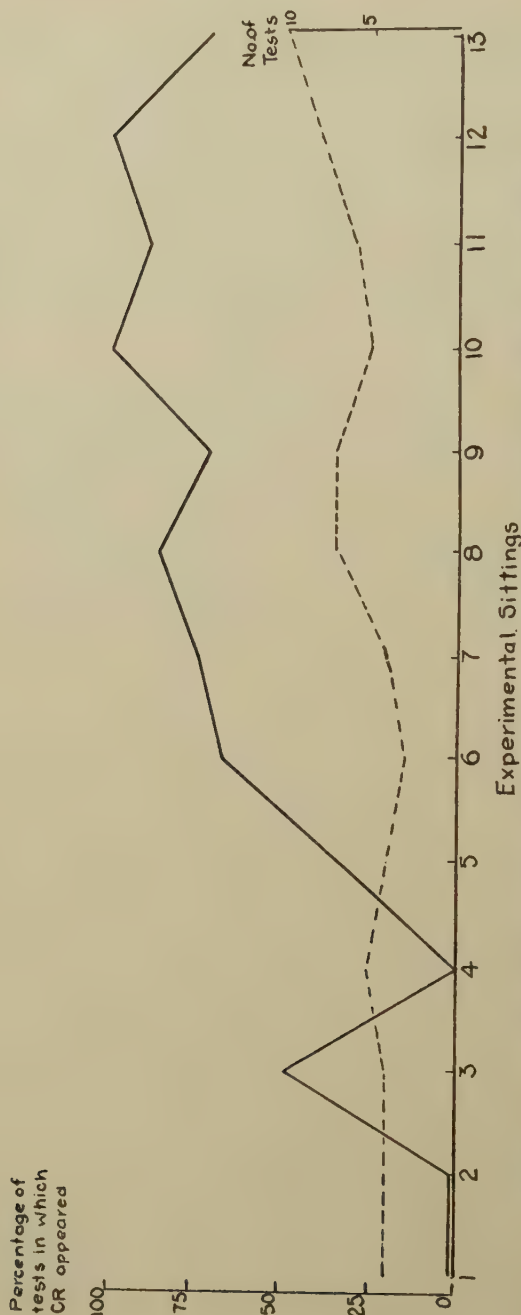


FIGURE V. PERCENTAGE OF TESTS IN WHICH CONDITIONED RESPONSES APPEARED (SUBJECT HIR).

The curve shows the percentage of the total number of presentations of the left stimulus alone in which contraction of the right quadriceps occurred. Only during the third sitting were these responses of the short-latency bilateral type. The broken line indicates the number of tests during each sitting.

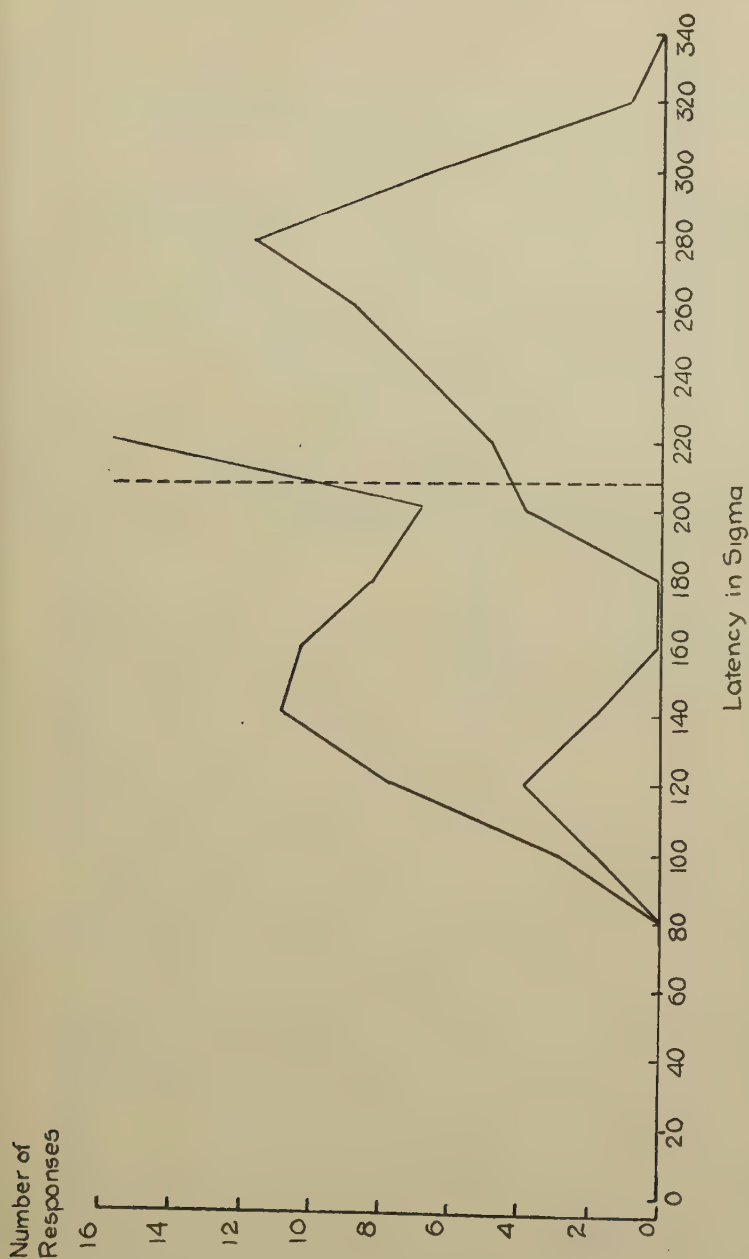


FIGURE VI. DISTRIBUTION OF LATENCIES OF CONDITIONED RESPONSES (SUBJECT HIR).

The upper curve shows all cases of pre-stimulation contraction of the right quadriceps during the double stimulations.

The lower curve shows all cases of conditioned responses during the tests where the left stimulus was given alone.

The vertical broken line indicates the incidence of the stimulus during the double stimulations.

2. No instances of long-latency responses were observed to be bilateral.

3. Its recruitment period is typically longer than that of the shorter latency response. Comparing recruitment periods of three types of responses we have: reflex—40 sigma, shorter latency bilateral response—60 sigma, long-latency response—100 sigma. The recruitment period is variable, and in some instances may be much lengthened.

4. The height of the contraction is usually ample. A contraction of three times the average normal reflex was recorded. In some cases, however, the contraction was very slight.

5. The contraction-curve was smoother and of greater duration than in the case of the shorter-latency responses.

6. The response could be present in the absence of any appreciable reflex response of the leg stimulated (Plate IV, cut 4).

7. The response could be present along with a preceding short-latency response (Plate IV, cut 3). Although the short-latency response in these cases was usually unilateral, one record shows, after the point of stimulation of the left muscle, the following: (a) reflex contraction of the left quadriceps, (b) bilateral response consisting of (1) secondary contraction of the left quadriceps with latency of 152 sigma and (2) slight concomitant contraction of the right quadriceps with the same latency, (c) strong contraction of the right quadriceps 270 sigma after the stimulus. The long-latency response may thus be present along with shorter-latency response of the same muscle.

8. This type of response showed three instances of true generalization. Percussion of the right tendon alone was in these cases followed by a long-latency response of the same leg. No long-latency secondary contractions of the left quadriceps occurred at any time.

9. No backward conditioning (*i.e.*, contraction of the left quadriceps on percussion of the right tendon) of this type of response was recorded.

10. Long-latency responses occurred under instructions to inhibit the kick.

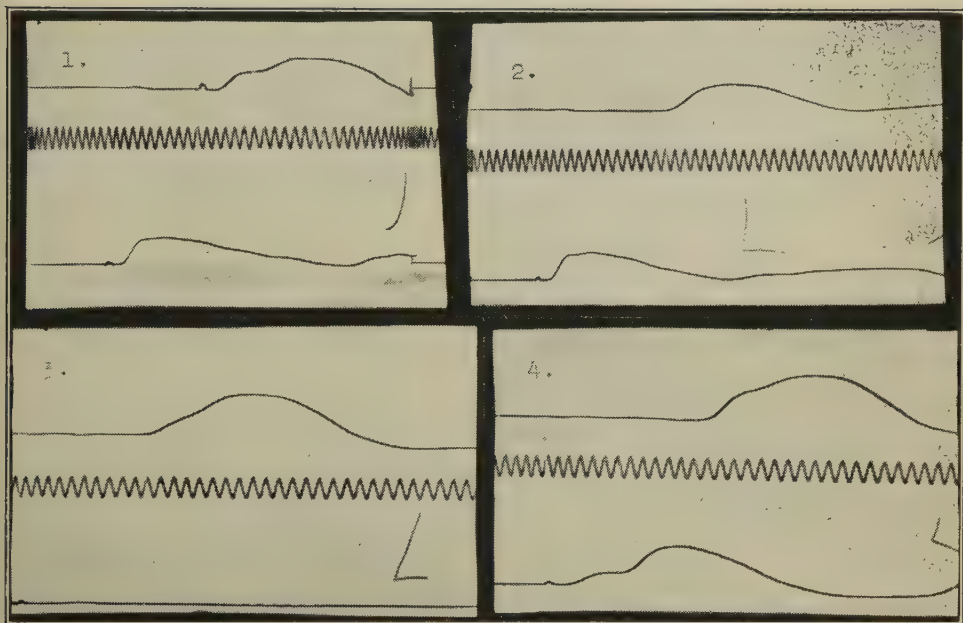


PLATE IV. LONG-LATENCY CONDITIONED RESPONSES OF SUBJECT HIR.

Cut 1. Long-latency response showing during the double stimulations as secondary contraction of right quadriceps.

Cut 2. Long-latency response during test where left stimulus alone was given.

Cut 3. Long-latency response along with very slight reflex response to left stimulus.

Cut 4. Long-latency response along with unilateral secondary contraction of left quadriceps.

11. The response was present during the double stimulations. It then showed as facilitation of the reflex, pre-stimulation contraction just before or just as the blow fell and as secondary contraction of the right quadriceps.

Results of Experimental Extinction

During the last five sittings observations were made of the effects of the discontinuance of double stimulations. Fifteen double stimulations given at the beginning of the first sitting of the "extinction" period showed that conditioned responses were present as in the preceding sittings and served to re-establish any loss from the day before. After this short period of double stimulations, the single stimulations of the right and left leg were begun, the blows being given in random order at $\frac{1}{2}$ minute intervals.

Long-latency response of the right leg to percussion of the left occurred three times. It was not observed during any succeeding trials during the extinction period.

The short-latency response, showing as secondary contraction of the stimulated muscle, continued to appear over a period of three days during which 404 single stimulations were given in five experimental sittings. It was apparently as strong at the end of this period as at the beginning. Cut 4 in Plate III is the last of the responses given at the 404th single stimulation. It is seen to be very active with almost complete absence of reflex response. Strong secondary response was frequently found along with weak reflex primary contraction throughout the extinction period. An occasional active reflex was recorded, but was the exception rather than the rule. This was true of the records of each leg.

One hundred single stimulations were given during the first sitting of the extinction period, 100 during the second and 170 during the third, the interval between stimuli being somewhat shortened at this sitting. In the next sitting, after 6 single stimulations, an attempt was made to test for facilitation effects at various intervals by the method described in section IV. The right blow preceded in half the trials while the left preceded in the others. Since the secondary contractions continued to appear on the curves, thus interfering with any possibility of distinguishing a difference in facilitation effect at

different intervals, the attempt was given up after 22 double stimulations. An attempt at extinction was then made by a reversal of the order of stimulation, applying paired stimuli at 1/5 second stimulus interval in the order right-left.³³ Secondary contractions of the right quadriceps continued with unchanged frequency through 72 such stimulations. At the end of this sitting, when single blows were again administered, and at the beginning of the last sitting, the same phenomenon continued. The response was apparently unchanged by the long attempt at extinction.

The last part of the last sitting was taken up with voluntary reactions. These are treated in the next section.

Amplitudes of Response

The amplitudes of response showed marked changes throughout the conditioning period as has been mentioned several times. In dealing with the amplitudes of response there are two possible measures of many of the curves. First there is the primary reflex itself whose peak comes about 100 sigma after the blow. Then there is the secondary response the peak of which comes 200 sigma or more after the blow. In treating amplitudes of response the changes in the two must not be confused.

The primary reflex response of the left leg (original response to the conditioned stimulus) showed large variations both above and below the average normal. (By "average normal" is meant the average amplitude as determined during the adaptation period.) The greatest average amplitude of this response was during the ninth sitting of the conditioning period. Previous to this it had been low during several sittings, and throughout was occasionally slight or absent along with strong secondary contraction. At the tenth sitting and at all succeeding sittings the reflex response to this stimulus was usually very slight. It was because of occasional active reflexes that the averages were kept up. But during the 10th, 11th, 12th and 13th sittings the amplitude was but 33% of the average normal for that leg.

The response of the right leg was affected in the double stimulations by facilitation of the preceding blow to the left.

³³ The effect of double stimulation in either order is probably reinforcing.

The amplitude of this facilitated response showed an upward trend throughout the conditioning period. During the first sitting of the conditioning period it was 145% of the average normal as determined for the adaptation period, while during the 13th it was 237% of the average normal.

On the other hand, the unfacilitated response of the right leg showed a trend toward reduction in the primary reflex response. This reduction became progressively greater until in the last three sittings of the conditioning period the average amplitude of the reflex contraction of that leg was but 14% of the average normal. The amplitude of the reflex continued low throughout the extinction period. With this reduced reflex contraction there was usually present a marked secondary contraction as described above.

Automaticity of Response

The complete automaticity of the phenomena described cannot be questioned. The subject was so occupied with his reading that he had very slight awareness of the experimental procedure. After the first few sittings he ceased taking any interest in what was being done, and by the end of the 20-hour period he was not even aware of what had been done. It was, of course, impossible for the subject to know that the right leg occasionally kicked before the blow fell.³⁴ Such fine time discrimination is not present in this type of reaction.³⁵ The delayed response of the leg in those cases where there was slight reflex contraction and strong secondary contraction was equally out of the subject's awareness. It was only in those cases where crossed response took place at the presentation of but one stimulus that the subject could be aware of having made such response. At the end of the sitting where this first occurred the subject commented on it, "Once when you hit only one leg, the other kicked up of itself. I *was* surprised!" Similar unsolicited remarks about the automaticity of the response were made after other sittings.

³⁴ Subject Rbw made such pre-stimulation reactions in almost 300 instances over a period of six months, yet was surprised later to hear that she had made them.

³⁵ In the facilitation tests the subjects were of the opinion that most of the blows were simultaneous, a few separated by an interval. The subjects in the conditioning experiment were questioned at the close of the sittings. They were usually uncertain whether the order of the blows had been left-right or right-left.

Results of Other Subjects

The results obtained from other subjects are confirmatory of those which have been described in detail from the records of subject Hir. In the case of no one subject, however, is the completeness of the results comparable to those of Hir. It is unfortunate that, of the other three subjects who served over a long period, two showed relatively infrequent modification of the knee-jerks (Mon and San), while the other (Rbw) continued throughout all sittings to give bilateral responses regularly, showing neither a loss of the crossed component nor a development of long-latency conditioned responses.³⁶ In the case of those subjects who served for shorter periods the results are of insufficient number for comparison, but taken as a whole they complete the picture of the phenomena already described. There is general confirmation of the results of Hir with certain added facts.

Short-Latency Conditioned Responses

One subject (Asc) normally showed slight crossed extension. Of 29 subjects tested in the present apparatus he was the only one showing such crossed contraction of the quadriceps to tendon percussion *before* double stimulations. In his case it occurred in four of twenty single stimulations. It was obviously the same short-latency response present in other subjects only as a result of double stimulations. The contractions were bilateral and of short latency (119, 146, 150 and 158 sigma). The crossed component was weak, probably resulting in little displacement of the leg.

If all cases of crossed quadriceps contraction after double stimulation be considered as conditioned responses (ignoring for the moment the fact that the bilateral responses and long-latency responses seem to be different phenomena), the results of these other subjects show that the appearance of the first conditioned response might take place after greatly varying numbers of combined stimulations. In one case (Raw, aged 16) there was strong bilateral response at the second double stimulation. In subject Harm the first response of this kind occurred in the third stimulation; with subject Rbw in the

³⁶ For this subject the sittings were spread over a period of six months. This may account for the failure to show the changes which Hir showed with daily sittings.

fourth stimulation. In other subjects of this group crossed contraction occurred after 20 to 195 double stimulations. (See table V.)

In two subjects no conditioned responses were observed after 326 double stimulations in one case (Schi) and 50 double stimulations in the other (Raz). Although there were no conditioned responses, evidence of modification in the case of subject Schi was present in the form of a decrease of the facilitating effect (previously pointed out in section IV). In subject Raz the facilitating effect of the preceding stimulus was slight.

Five subjects (Schu, Asc, Dur, Mad) made voluntary reactions for a period and were then given double stimulations. Under these conditions crossed quadriceps contraction during the double stimulations would be placed under the category of habit rather than of conditioned responses.³⁷ The results of these subjects showed: 1) crossed contraction was either present in the first double stimulation or developed very readily, 2) *the character of these responses was in no way different from the short-latency bilateral responses developed in other subjects by the conditioning technique.*

Eleven of the other subjects made voluntary reactions after a period of conditioning or facilitation tests. The results showed the same facts. 1) Bilateral responses became more frequent after voluntary reactions. 2) They differed neither in latency nor in form from those given before voluntary reaction, when they had been due to conditioning alone. Three of these eleven subjects were exceptions to this, showing no automatic crossed responses after making the reaction voluntarily. It is important to notice that two of these (Harr and Schi) were the two subjects for whom the preceding stimulus had an inhibitory effect, while the other (Bro) was normally without a knee-jerk except under strong facilitation.

Taking all the subjects into account there were: a) ten in whom bilateral responses were developed by double stimulation, b) two in whom double stimulation did not result in

³⁷ Dodge found that voluntary contraction of the quadriceps to tendon stimulation resulted in a habit which persisted. "The knee-jerk for instance may be voluntarily reinforced by additional arbitrary contraction of the leg extensors. This reaction may become by a little practice the habitual response to the same blows on the patellar tendon that produce the reflex." *Psychol. Rev.*, 1926, 33, 4-5.

crossed contraction, c) five in whom automatic bilateral responses were made after a period of voluntary reaction, d) nine (already included in a) in whom bilateral responses increased in frequency subsequent to a period of voluntary reaction and e) three in whom a period of voluntary reaction did not modify the reflex pattern (one of these being also included in b).

Analysis of the data of each subject shows that the greatest factor favoring easy formation of this bilateral response is the presence of strong facilitation of the second response by the preceding blow. Those subjects in whom the effect was inhibitory (Harr, Schi) did not give such responses. Subject Harm gave bilateral responses at the first and third sitting, but at the second when the painful first blow caused inhibition of the second response, he gave no bilateral responses.³⁸ Of the subjects in whom the facilitating effect of the blow was slight, one (Raz) gave no bilateral responses, the other (Lyo) gave but one during the double stimulations. Strong facilitation combined with an attitude of tenseness seemed to be the factors chiefly favoring early and frequent occurrence of these responses.³⁹

The character of the short-latency responses was found to be much the same for each of the subjects.

1. It was found to be generally true that the response was made to either of the two blows.

2. Its latency was typically brief. There were, however, large individual differences in the median value. For subject Raw the median latency of these responses was 128 sigma. What the upper limit of latency for a given subject might be is not determinable from the results because of the difficulty of distinguishing between these responses and the long-latency responses. It is safe to say, however, that in some subjects the median was as high as 190 sigma. In the case of subject Rbw there were 324 bilateral responses from which the latency could be computed. These were found to cluster very closely around their median value of 140 sigma. The normal range

³⁸ It is probable that inhibition of this kind can be conditioned as well as excitation. If relaxation was present, the recording system was not delicate enough to show it clearly.

³⁹ Tenseness of the subject may be considered as providing additional facilitation.

in this case was 110 to 175 sigma, while the 25th and 75th percentiles were at 120 and 150 sigma respectively.

3. It will be recalled that in the case of subject Hir these responses were found to be at first usually bilateral, then with increasing frequency unilateral. Although the other subjects do not show clearly a dropping out of the crossed component, there was usually an increase in the number of unilateral responses, the proportion of bilateral responses decreasing in the later sittings. In some subjects the unilateral reaction was clearly present before the first bilateral contraction was recorded.

4. The recruitment, amplitude and duration of the responses was found to be as described for subject Hir. In subjects Raw and Rbw the crossed reaction was exceedingly active, both amplitude and steepness of rise being close to that of the reflex.

5. Short periods of attempted experimental extinction were tried with all subjects who showed modification of the reflexes. Though some of them, showing these phenomena infrequently, showed few or none during the stimulation by single blows, in others the short-latency responses continued to be made during this period. The first effect of the discontinuance of double stimulations was usually the dropping out of the crossed component of the bilateral reaction, with subsequent unilateral secondary response. This might continue until the end of the 20 single stimulations. In subject Rbw the bilateral responses were found to be given to single stimulation after lapses of three and four days during which no sittings took place. This subject was tested each month for a period of six months, and, though the responses were not present to single blows after the lapse of a month, they were easily redeveloped by double stimulation and then occurred regularly.

Long-Latency Conditioned Responses

That the responses were of two kinds, the one bilateral and of short latency, and the other unilateral and of considerably longer latency, was also indicated in the results of some of these subjects. The interpretation of the data, however, was necessarily made on the basis of qualitative differences in the responses and from an observation of their behavior, for in

none of the subjects was the total number of the responses sufficient to show a clear bimodal distribution of the type found in the case of subject Hir (see Figure VI). With three subjects (Harm, Fje and Mon) it is clear that there are two types of response. In subjects Ste, Gol and San it is also indicated. The latter seemed to give mainly the longer-latency type of response. The late development of the long-latency reactions was true of these six subjects as it was of Hir, the first such responses appearing after 46, 116, 134, 157, 170, 172 and 316 double stimulations (the last figure being for Hir). Qualitatively the responses were like those of Hir.

A true notion of the response latencies cannot be given by any measure of central tendency of the results, being possible only from careful analysis of the original records. In Table V the median latencies of the responses made during the tests of the application of the "conditioned" stimulus are presented. For some subjects, of course, these figures include both long- and short-latency responses so that the median value is true of neither. Reference to the results of Hir in the table readily shows this to be the case. They do, however, serve to indicate roughly the trend of the results. In the cases of subjects Rbw and Raw it was possible to include not only the responses made during the tests, but all the pre-stimulation contractions, since no responses with a latency greater than the stimulus interval were recorded. In the cases of subjects Mad, Lon and Gol the conditioned responses were made during tests for facilitation effects so that they were not a true sample of the distribution.

Amplitudes of Response

In no other subject was there a reduction in the amplitude of the primary reflex part of the jerk to the extent found after the tenth sitting in subject Hir. There were in some subjects, however, occasional responses in which the reflex was slight along with strong secondary contraction. These were especially numerous and striking in the case of subject Rbw. There were many instances here of both bilateral and unilateral secondary responses with slight reflex contraction.⁴⁰ The reflexes of this subject had normally been very active.

⁴⁰ Changes in the amplitude of the knee-jerk are especially difficult of interpretation, and in the present instance where there are several factors affecting the amplitude, variations in the height of the jerk can easily be misinterpreted. Therefore only the more striking variations have been noted here.

TABLE V

<i>Subject</i>		<i>Latency of cond. responses</i>	<i>Number of cond. responses</i>	<i>Double stim necessary to condition</i>	<i>Number of pre-stimulation contractions</i>
Hir	25th % tile	210			
	median	247	53	2	62
	75th % tile	275			
Mon	25th % tile	245			
	median	252	13	116	20
	75th % tile	272			
San	25th % tile	268			
	median	307	8	70	7
	75th % tile	350			
Rbw	25th % tile	120			
	median	140	324*	4	*
	75th % tile	150			
Ste	25th % tile	302			
	median	335	8	99	0
	75th % tile	345			
Lyo		182	1	195	0
Fje	25th % tile	178			
	median	205	16	71	2
	75th % tile	275			
Harm	median	260	4	2	18
Raw	25th % tile	119			
	median	128	17*	1	*
	75th % tile	135			
Schi			0		0
Raz			0		0
Schu	25th % tile	185			
	median	215	16	13	51
	75th % tile	225			
Asc	25th % tile	132			
	median	144	16	0	65
	75th % tile	161			
Mad	25th % tile	130			
	median	131	8†	†	
	75th % tile	146			
Lon		150	1†		
Dur		182	3†		
Gol	25th % tile	198			
	median	235	10†		
	75th % tile	300			

*No responses over 200 sigma so all could be figured into medians.

†Responses made during tests for facilitation effects.

Automaticity of Responses

The complete automaticity of the responses was true also of these subjects. No subject was aware at any time of the pre-stimulation contractions of the opposite leg though many were recorded. The spontaneous remarks made during and after the sittings show the reactions to have been automatic. As examples: Subject Fje remarked after the second sitting, "My leg kicked up without being hit today. I didn't know it until my heel struck when my leg came down." Subject Lyo exclaimed on making a conditioned response, "What the devil! How did that happen?" Subject Asc had during the second sitting made a crossed response each of six times single blows were given. Questioned after the sitting it developed that he had not even been aware that the second blow had at any time been omitted. He thought that in each case his leg had reflexly responded to tendon stimulation.

The possibility of inhibiting the response was tested in but two of these subjects. These, both graduate students in psychology, adopted the method of relaxation which resulted not only in absence of conditioned responses but also in marked reduction in the reflex response.

*Discussion of Results**A. Short-Latency Responses:**Relation with normal knee-jerk:*

That the discharge which gives rise to the bilateral and unilateral contractions is present normally during the knee-jerk is indicated by (a) the presence of marked facilitation of the knee-jerk by a contralateral stimulus as shown in Section IV and (b) the presence of bilateral responses (and probably unilateral secondary contractions of the kind described) in some normal individuals.

(a) The relation of these responses to the discharge giving rise to the facilitation effects described in Section IV cannot be seriously questioned. The results seem to point to this so conclusively that no further discussion will be undertaken. The bilateral responses are without doubt an exaggeration of a discharge which is normally subliminal for contralateral contraction and gives rise only to facilitation through summation with the reflex.

(b) One subject (Asc) before conditioning gave an occasional short-latency bilateral response.⁴¹ In subjects with active reflexes the knee-jerks frequently showed a clear secondary contraction in the first few responses tested. There is no indication in the present results that this secondary response on the normal reflex is of different origin from that observed so strikingly after conditioning. The presumption is strong that the same discharge is present in all normal knee-jerks.⁴² From its temporal incidence there is justification for ascribing the "hump" usually present on the descending limb of curves of muscle thickening in the knee-jerk to the arrival of such a discharge.* The appearance of the secondary contractions developed by conditioning is such that no point can be designated at which they may be said to begin. They grade imperceptibly into responses which must be classed as normal knee-jerks. Their identification, therefore, is a matter of relative amount of secondary response: small secondary response is normal, large secondary response is conditioning. Subjects normally differ considerably in the prominence of the hump on the descending limb of the jerk, but its presence is general. Its absence is indicated in cases of "spinal" knee-jerks in man and in the knee-jerks of infancy where higher levels may not yet be functional. It therefore seems possible that the responses are an exaggeration of a normal component of the knee-jerk. This may be, in part, what is known as the "tonic" phase of the jerk. The rapid conditioning shown by some subjects under the present methods may be attributed to the normal presence in their cases of a bilateral discharge which is almost liminal for contraction.

⁴¹ The early observations of Gotch (1896) on crossed extensor reflexes to tendon percussion in an abnormal patient indicated bilateral response. They seem to be the same phenomenon here observed. Gotch reported similar latencies. Stewart (1897) reported latencies of 126 sigma for a crossed adductor response. It is possible that he was actually measuring crossed extension as in the present investigation.

⁴² See Travis, Tuttle and Hunter (1927) for a study of action currents in the normal knee-jerk. They interpret their results to indicate the presence of two discharging centers during the jerk. The earlier results of Snyder (1910) are also interpreted as showing a dual discharge, the second element of which has a temporal incidence similar to the secondary contractions observed in the present investigation.

* The "hump" may also be caused in part by a stretch stimulus resulting from the sudden relaxation of the muscle. The descending limb of the curve of muscle thickening is probably a result of complex factors.

Conditions of Appearance:

A bilateral response appeared with greater or less frequency in 15 of the subjects. The results indicated that the conditions favorable for such a response were (1) an attitude of tenseness, (2) the presence normally of strong facilitation of response by a preceding contralateral stimulus and (3) repeated successive stimulation of each side. The effect of tenseness of the subject probably acts by raising (by summation or other means) the excitability of the centers involved. Strong facilitation of a contralateral response by a tendon stimulus is evidence of the normal presence (subliminally) of the same discharge which gives rise to bilateral responses. The combined stimulations act to increase the magnitude of this discharge to the point where response is produced.

That the procedure of eliciting the two knee-jerks in close temporal succession develops bilateral conditioned responses seems to fit in with known facts of conditioning and may be explained in terms of current theory of conditioning. The situation may be put as follows. The muscle stretch normally gives rise to a rapid reflex response and to a secondary response (the normal hump and the facilitation effect) mediated through some higher level center. A part of this secondary response is a subliminal discharge to the center operating in the contraction of the contralateral quadriceps. When, now, the stimulation of one side is closely followed by stimulation of the other, the crossed discharge acts by summation to increase the response of that side. Repeated successive activation of the two responses makes possible a supra-liminal crossed discharge. The situation is thus analogous to one in which auditory stimulation becomes supra-liminal for salivary secretion through repetition of successive excitation of these two sets of receptors.

The bilaterality of the response must be attributed to the close functional connection of the centers giving rise to the secondary response of each side. The increase of the homolateral component of the discharge along with the appearance of the crossed contraction is comprehensible if we look upon the normal discharge as being bilateral. The effect of conditioning, therefore, is to increase the magnitude of the whole response. The homolateral component is normally present and by far the stronger of the two. We may expect it as a

result of conditioning to show greater increase than the crossed reaction to which there is relatively high resistance.⁴³

The apparent dropping out of the crossed component of the reaction, as shown especially in the records of Hir by a decrease in the bilateral responses and a great increase of homolateral secondary contractions, cannot be definitely explained as due to the operation of a selected factor. There are at least three possibilities: (1) that the crossed component shows negative adaptation, (2) that there is an adjustment of the crossed response to the length of the stimulus interval, (3) that with the development of the long-latency response the afferent impulses giving rise to the crossed component of the short-latency response are circuited through higher levels so that it drops out similarly to the reflex response to the first stimulus.

Negative adaptation of the crossed component can conceivably arise since the stimulus interval was such that the second reflex came at a time (235 to 250 sigma after the first blow) falling outside the normal range of latency of the bilateral response. The explanation by negative adaptation seems to be favored by the previously discussed fact that the facilitating effect of a preceding stimulus shows a daily decrease in some subjects. (See Section IV.) At first sight, negative adaptation is not indicated by the results of Hir, in whose case the loss of the crossed component was most obvious. In his case there was an increase in the amplitude of the facilitated second jerk throughout the conditioning period. This seems to indicate an increase in the crossed component rather than a decrease. It could be explained by assuming (1) that the impulses in the crossed component have become asynchronous (thus failing to evoke contraction) with lengthened after-discharge so that the incidence of their greatest facilitating effect would continue over a longer period, (b) that the discharge of the center was delayed by an amount sufficient to adjust to the stimulus interval, thus increasing the facilitating effect and appearing as the long-latency conditioned responses of the later sittings, or (c) that the increased facilitation was due to the increasing importance of impulses coming from some other center active in the production of the long-latency responses.

⁴³ Resistance to crossed reflexes is greater than to homolateral reflexes.

The determination of the true reason for the loss of the crossed component requires more evidence than is available from the present results. So far as the results go, however, they point to negative adaption as the best explanation.

The results showed clearly that the performance of a voluntary crossed response to the tendon stimulus effected an integration of the tendon stimulus with a bilateral response of the same character as that developed by conditioning. The voluntary performance of the response seemed to be a more efficient procedure for setting up automatic responses than is involved in the conditioning procedure. The result of the two methods is the same: the *habit* appeared in no way different from the *conditioned response*. The integration effected by volition⁴⁴ is the same as that effected by combined stimulation. In combined stimulation the second blow was the reinforcing stimulus which made possible the modified knee-jerk pattern, while in voluntary activity the discharges of voluntary origin may be looked upon as taking the place of those set up by the second muscle stretch.* The similar results of the two procedures indicates that the integration was the same in each case.

B. Long-Latency Responses:

The development of the long-latency responses may be explained by either of two mechanisms.

(a) These responses may be due, as pointed out above, to an adjustment to the stimulus interval which results in delay of the discharge of the crossed component of the bilateral reactions. Such a hypothesis is possibly favored by the fact that in subject Hir, the facilitating effect of the preceding stimulus increased during the conditioning period. Against it are the facts: (1) that the results of combined stimulation was in most subjects a reduction of facilitation indicating a loss of crossed effect, (2) that, in isolated instances, records showed that the shorter-latency discharge might be bilateral with a

⁴⁴ The use of such terms as volition, awareness, attention, etc., by the writer should not be construed as assigning causal efficacy to psychic events. They are used only to denote those sequences of objective events which common usage has associated with them. Thus, for instance, in this investigation a subject has been regarded as making voluntary reactions if he has been so instructed and if he has reported verbally or by other means that his reactions were voluntary.

* In this case, therefore, the instructions to the subject function as the "unconditioned stimulus."

long-latency discharge also present, (3) that in Hir a reduction of the stimulus interval to 140 sigma apparently caused increased activity of the bilateral responses with no concomitant decrease in the long-latency responses.

(b) A more plausible explanation is that the long-latency response is a new conditioned response arising from another center (possibly of "higher level") than that involved in the faster bilateral responses. The fact that these responses were always unilateral and given only by that side which received the second of the two blows indicated that the discharge was not from a center with a normal bilateral action. In the case of Hir the bilateral responses had been infrequent during several sittings before the development of the long-latency responses was strong.⁴⁵ All the characteristics of these responses (the greater latency, the slower recruitment, the smoother curve, the greater duration, etc.) seem to show them to be distinct from the bilateral responses.

If these long-latency responses are the result of a functional mechanism distinct from that which initiated the short-latency bilateral contractions, it may be that they are due to some stimulus other than the muscle stretch. It is conceivable that the short-latency bilateral response is initiated by afferent impulses set up by the muscle stretch, while the long-latency response is the result of the stimulation of tactual and pressure receptors at the knee, and the diffuse tactual-kinesthetic stimulation from the slight jar to the body. On the other hand, the stimulation might be the muscle stretch, but the integrational level be a higher one than for the short-latency response. The apparent difficulty of establishing the long-latency conditioned responses points to a conditioned stimulus of slight intensity. Introspectively it is true that the blow on the patellar tendon does not have the vividness which is true of visual, tactual and auditory stimulation. The main factor, the muscle stretch, gives rise to almost no sensation, one's awareness of it being due largely to accompanying stimuli not essential to the reflex. It may be that this is an important factor determining the

⁴⁵ This would be an argument against considering the long-latency response as due to delay of the crossed component of the bilateral response. If this delay took place, we would have to account for the fact that though the shorter-latency crossed response was infrequent after the third sitting, the long-latency responses did not appear regularly until the sixth and seventh sittings.

speed of the development of the long-latency conditioned response.⁴⁶ The conditioned knee-jerk to sound stimulation, as shown in Schlosberg's illustration, resembles the long-latency responses of the present results far more than it does the shorter-latency responses. This, again, may point to an essential difference between the two types of responses either in stimulus or in level of action.⁴⁷ *It implies that the short-latency response may be a conditioned response to the muscle stretch itself or a conditioned response involving reflex arcs already present, while the long-latency conditioned responses are the result of other stimulation elements or higher level elaboration of the stretch stimulus.*

The difference between the two would not be an essential difference, but a relative difference in closeness of the original association on each level. The reflex knee-jerk, the short-latency conditioned response and the long-latency conditioned response may represent three levels of control over the reactions of the responding muscle. Integration of the responses of both sides is indicated to be possible only on the two higher levels.

C. Permanence of the Conditioned Responses:

The unilateral secondary responses were found to be relatively permanent, persisting in one subject through at least 400 single stimulations and in another over an interval of as much as four days. This permanence is unusual in conditioned responses and, coupled with the rapid extinction of the long-latency response, it points to a different functional mechanism for the two. The permanence of the responses seems to indicate that the conditioning was possibly specific to the experimental situation. The environment of the screened chair, the leg-rests, the reading matter, the ear-phones, etc., may have been a necessary part of the stimulus complex for their elicitation. The dropping out of the reflex response with the exaggeration of the secondary response is obviously a mal-adapted response which would interfere with locomotion to

⁴⁶ Hamel believes conscious elements to be a necessary condition for the development of conditioned responses. Schlosberg ascribes the difficulty of conditioning and lack of stability of the conditioned knee-jerk largely to the lack of conscious prepotency of the reflex.

⁴⁷ Conditioned responses to sound were developed in a preliminary investigation. Their contraction-curves were found to resemble those of the long-latency responses.

some extent. No disturbances of normal locomotion were reported by the subjects. An attempt to test for the presence of these responses when the subject was not in the chair met with no success for lack of suitable recording means. The permanence of the response during the extinction period indicates further that this modification of the reflex pattern is different from the conditioned responses usually described. It looks as though this response were an exaggeration of a reflex discharge normally present in the knee-jerk so that it does not show negative adaptation to a marked degree.

D. Automaticity of the Conditioned Responses:

It is the opinion of the writer that the automaticity or non-automaticity of these conditioned responses is not the question at issue. Of their complete automaticity there seems to be no reasonable doubt, since the subject claims them to be so, is often unaware of their occurrence and may be unable to prevent them. The introspective criterion of volition or the objective one contained in the instructions to the subject are the only ones we can have in the present situation. The question, "Are the conditioned responses voluntary?" can obviously be answered in the negative. The important question for experimental analysis is whether the objective character of the conditioned and voluntary activity are so closely similar that they can be attributed to the same functional mechanism.

E. Amplitude Changes:

The great decrease in the amplitude of the reflex portion of the knee-jerk, as found in the later sittings of subject Hir and in some of the responses of the other subjects, is in accord with the results of animal conditioning (see Razran, Borovski). The original response to the conditioned stimulus, even when this is electric shock (Erofeeva), is found to become minimal as the conditioned response becomes established.⁴⁸

The knee-jerk does not seem to show amplitude changes as a result of repetition alone. Dodge (1927) found that the elicitation of 1032 responses over a period of two years resulted in no change in the extent of muscle thickening. In the

⁴⁸ This, in part, has led to the explanation of conditioning and related phenomena on a theory making use of a drainage hypothesis (see Pavlov, Woodworth, Razran).

case of subject Mon in the present experiment no change in the amplitude of response was observed as a result of 100 single stimulations on each of three successive days. On the other hand, in those subjects where *double* stimulations were used (both in conditioning and in facilitation tests) there was ordinarily a decrease in the extent of the jerk. Although caution is necessary in the interpretation of such amplitude changes as being the result of any one selected factor, it seems probable that double stimulation, as in the present experiment, results in reduction of the knee-jerks. Toward this reduction two factors may contribute: (1) a re-routing⁴⁹ of the afferent impulses from the reflex portion of the response into the secondary response, (2) a reduction in the magnitude of the un-facilitated reflex response when the habitual preceding contralateral stimulus is omitted. This latter may arise when summing impulses are usually present along with the reflex, and the arcs thus become less efficient in mediating response without the presence of these aids.⁵⁰

Conclusions

Conditioned responses developed by the repeated successive elicitation of a knee-jerk from each leg were of two types.

(1) The most frequent was a bilateral response with a typically brief latency of 130 to 190 sigma. The response developed readily in some subjects. It might be unilateral, the crossed component failing to arouse active contraction. It tended to become unilateral on repetition of double stimulations. The response was given to either stimulus. It was found to be very resistant to experimental extinction. The discharge giving rise to it is the same as that concerned in the production of the main facilitating effects described in Section IV. The same discharge is probably present in the normal knee-jerk, showing as the "hump" on the descending limb of the curve.

Voluntary crossed extension of the leg to a blow on the tendon resulted in a habit which continued when the subject's

⁴⁹ Dodge uses the term "resystematization." It seems especially applicable to the modifications described in this paper.

⁵⁰ See footnote concerning the results of Mon, Section IV, p. 26. Results are there given indicating that the response to the second of paired stimuli is subnormal when the facilitation of the second is absent.

attention was distracted from the stimuli. This habit was similar in all respects to the conditioned responses developed without volition.

(2) The second type of response developed with difficulty. It occurred only in the case of some of the subjects. Its latency was typically 100 sigma greater than that of the bilateral response, and its characteristics were different. It was a response of the opposite leg only and was usually specific to the first stimulus of the pair. It was probably mediated by a different discharging center. It disappeared rapidly in "experimental extinction."

In some subjects a marked reduction in the reflex response to stimulation took place as a result of conditioning.

SECTION VI. VOLUNTARY REACTIONS

Voluntary responses have usually been found to have the same reaction-time as conditioned responses. Hamel (1919) reported that a conditioned withdrawal response (using shock as the unconditioned stimulus) had the same reaction-time as the voluntary response.⁵¹ Humphrey (1927), also using shock as an unconditioned stimulus, got similar results, finding the reaction-time of the conditioned response to be that of a so-called "discriminative reaction." Conditioned knee-jerks were compared to voluntary reactions by Schlosberg. In the case of three subjects the conditioned knee-jerks were found to have an average latency of 0.40, 0.34 and 0.28 second respectively and the voluntary reaction-time was similar. He further found that the character of the conditioned contraction of the quadriceps was not that of the typical reflex but very similar to the voluntary reaction.

Cason (1922, 1923) stated that he found conditioned eyelid responses to be reliably faster than voluntary winks. His conditioned stimulus was a sound normally subliminal for a reflex wink. Under these conditions the effect of the conditioning could have been to raise the excitability of the reflex arc so that the stimulus became supraliminal. His situation, therefore, is not exactly comparable to that of the other investigators. It has a closer similarity to the conditions of the present investigation where there was found to be a close connection between stimulation of one quadriceps and an automatic response of the other. Conditioning here, too, was found to act on the existent functional connections to increase their conductivity.

In the present investigation voluntary reactions were recorded by the same method used in recording the conditioned responses. Both the form of the responses and the reaction-time can therefore be compared. Voluntary reactions were taken both with the use of a ready-signal and under conditions which duplicated as nearly as possible the experimental situation under which the conditioned responses were made. Volun-

⁵¹ Hamel's experiment was so arranged as to put the subject in a problem-solving situation. It is probably incorrect to class it under the head of conditioning.

tary leg reactions to sound were also studied for comparison with those to a tendon stimulus.

Method

Reactions with a ready-signal: A momentary stoppage of the buzzing in the ear-phones⁵² was the signal to prepare for reaction. This was followed after one to two seconds by a blow on the tendon.⁵³ The subject was to respond to this as rapidly as possible by a kick of the other leg. He was asked to kick with a force about equal to that present in a normally active reflex kick. After each ten reactions a rest period was inserted. The total number of responses taken from each subject varied.

Reactions without a ready-signal: To secure voluntary reactions which would be more directly comparable to the conditioned responses, these were recorded under the same experimental conditions as were used in the conditioning experiment. The subject sat reading, being instructed to give all his attention to his reading but to kick each time he felt a blow⁵³ on the opposite tendon. He was further told that the intervals between stimuli would be varied. Variations similar to those used in the conditioning experiment were used. No rests were given during the period of making these reactions.

Under both situations the blow was occasionally given (without foreknowledge on the part of the subject) to the tendon of the leg which was to make the reaction.⁵⁴ These responses were thus comparable to those in the conditioning period made to the "unconditioned" stimulus given alone. In order to make the results further comparable, double stimulations were sometimes given, the second blow falling on the

⁵² In testing for voluntary reactions the sound-screen had to be intense. Secondary cues were found to be of much greater importance in voluntary reactions than in conditioned responses. The loud buzzing which was necessarily used probably acted in the voluntary reaction period to lower the reaction-time (see Jenkins).

⁵³ In each subject who had served in the conditioning experiment the leg stimulated was the one which had received the "conditioned" stimulus.

⁵⁴ Since the reaction in this case was made by the same leg as was stimulated, shorter reaction-times might be possible. Poffenberger (*Arch. of Psychol.*, No. 23) found the relation between hand and eye on the same side to be no closer, so far as reaction-time was concerned, than between hand and eye on opposite sides of the body. The situation is here analogous. Though measurements were few, no difference in reaction-time as between reaction to a contralateral or homolateral stimulus was indicated.

voluntarily reacting leg. The interval between these was varied so as to observe the effect of preceding, concurrent and intercurrent stimulation. All other situations used during conditioning were duplicated at some point in the voluntary reaction experiment.

Reactions to sound: Leg reactions were made to the cessation of the buzzing noise in the ear-phones.⁵⁵ A break key made possible an instant termination of this sound. The subject was given a ready-signal by touching the top of his head. The response at sound cessation was a rapid kick of one leg.

In the case of subject Mad reactions of the leg to a touch stimulus below the knee of the other leg were recorded. The stimulus was given by dropping the percussion hammer from 25 degrees against a wooden guard strapped to the leg.⁵⁶ The blow completed an electrical circuit for the measurement of reaction-time.

Reactions to a blow on the tendon were made by 16 subjects. Two of these (Rbw and Harr) made no reactions with the attention distracted by reading. For 13 of the subjects conditioned responses (or automatic responses after voluntary reaction) were available for comparison. For six of them there were data on facilitation effects at different intervals. Nine subjects made leg reactions to sound cessation.

Results

A. Voluntary leg reactions to a blow on the tendon:

The results were in general confirmatory of those of past investigators. *No essential differences between voluntary and conditioned responses could be discovered.* Voluntary reactions were found to be similar in latency, form and behavior under varied conditions to the conditioned responses. Just as two types of response were found to develop as a result of conditioning, so the voluntary reaction seemed to involve two elements which correspond to the short-latency and long-latency conditioned responses. These two elements were possibly present in each of the contraction curves. In most in-

⁵⁵ Holmes (Columbia U. 1923) and Jenkins (1926) found reaction-time to cessation of a light stimulus faster than to onset. Jenkins did not consider this a true difference, interpreting it as due to better sensory adjustment under the conditions of reaction to removal of a light stimulus.

⁵⁶ This also gave a slight jar to the leg and body.

stances, however, the two phases of the reaction were probably fused into a single curve so that the distinction between them was not sharp. The characteristics of the voluntary reactions were as follows:

(a) Introspective reports: Most of the subjects spontaneously testified that it was easy and automatic to kick to a blow on the tendon of the other leg. Subject Fje stated that after the first few reactions "it seemed almost as though my leg kicked by itself." Subject Bro had a similar experience. "The muscle seems to tighten before I make the kick. It feels as though the energy travels right across the cord and into the muscle." Subject Asc gave a very interesting introspective report. At one point in the sitting he misunderstood the instructions to react voluntarily while reading, thinking he was to sit passively reading. Several single blows were then given. To each of these the subject responded with a kick of the opposite leg. After four such responses made automatically he realized that he had not followed instruction and began to react voluntarily. He reported that *the reactions subsequent to his decision to react voluntarily were introspectively no different than the automatic reactions.*

The degree of the automaticity varied for different subjects. Some of them found the reaction no more automatic than other voluntary reactions. In those subjects where it was automatic there was also a voluntary element in it. This is illustrated by the remark of Bro that "My muscle seems to tighten before I can make the kick." Here the tightening of the muscle was automatic, but added to this was a voluntary kick.

(b) The character of the response: To compare voluntary and conditioned responses the curves selected for the comparison must be of similar amplitude. It is obvious that voluntary action will differ from automatic action in at least one important aspect: the range of voluntary action is far greater. A subject can easily kick voluntarily with such violence as to upset the apparatus. The contraction curves of a voluntary response may rise to considerable height and show two or more successive contractions (see Plate V, cut 2) or be much prolonged.

The contraction curves of voluntary and conditioned responses are further different in that the long-latency phase of

the voluntary response is found added onto a short-latency phase, whereas the two types of conditioned responses were usually found in isolation. The result of this is that voluntary reaction-time is determined by the short-latency response. The long-latency response is an added feature which shows clearly only in some of the curves.

The curve of contraction in moderate voluntary reaction is indistinguishable from that found in the short-latency conditioned responses. The voluntary reaction may be bilateral, especially during the first few reactions. (See Plate V, cut 2.) In some subjects it is usually bilateral. It further resembles the short-latency conditioned response in that the subject kicks to a blow on either leg, though the instructions mentioned only a blow to the opposite leg. Such responses are identical with the secondary contractions observed in the conditioning experiment. (Compare cut 3 in Plate V with cut 2 in Plate III and cut 2 in Plate II.) The voluntary reaction was found to behave toward preceding, concurrent and intercurrent stimulation of the reacting leg in the same way conditioned responses behave, a reflex response taking place when the blow fell before the crest of the voluntary response. No stimulus variations used in the period of voluntary reaction could be found to distinguish them from the conditioned responses made in the same situations.

The differences between voluntary reactions and conditioned reactions consist only of (1) the fact that the voluntary response has a greater range and (2) the fact that the voluntary response is relatively invariable, occurring at each stimulation.

The contraction-curves of the voluntary reactions show two phases analogous to the two kinds of conditioned responses. In the records of conditioned responses there were instances (described in the preceding section) where there was bilateral response of short-latency with a long-latency response added to the crossed component so that it showed as a further rise of the contraction of that leg. Reactions with such contraction curves were frequent in the voluntary reaction experiment. The muscle of the leg which was to make the voluntary reaction in these cases showed a slight but fast contraction and then a slower more violent contraction. There was first a small rise in the contraction curve and then a much more

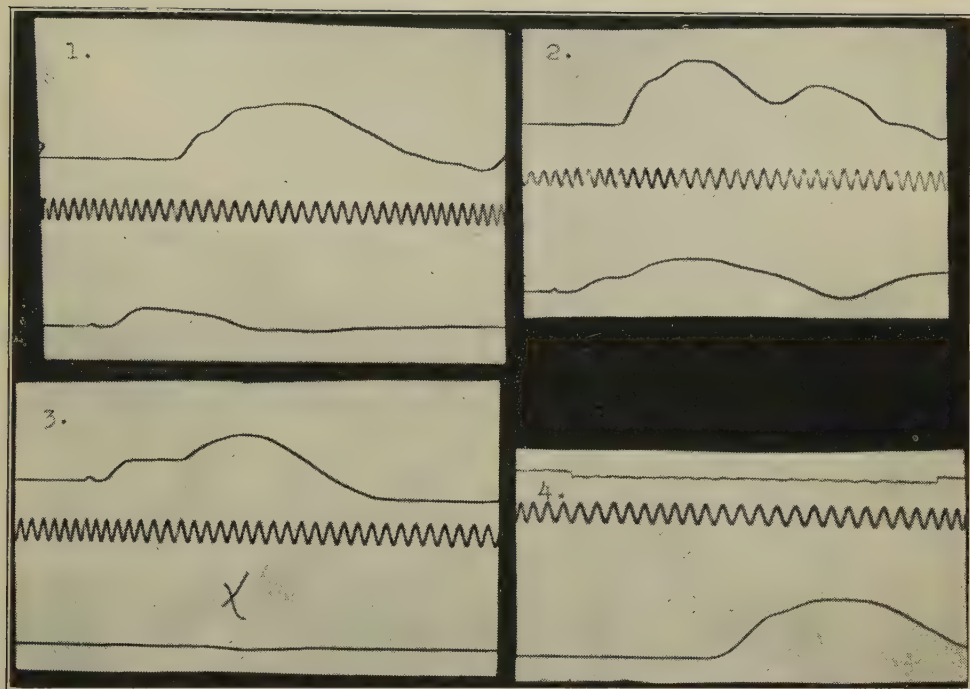


PLATE V. VOLUNTARY REACTIONS

Cut 1. Voluntary reaction to blow on opposite tendon (Hir).

Cut 2. Voluntary reaction to blow on opposite tendon showing that the response is bilateral. The response of the right muscle is strong and shows successive contractions (Hir).

Cut 3. Voluntary reaction when stimulus was given to right tendon. The reflex here precedes the voluntary response (Hir).

Cut 4. Voluntary reaction to sound cessation. Drop in signal line indicates duration of sound stoppage (Subject Lyo).

marked response. These latter responses are reminiscent of the long-latency conditioned responses described in the preceding section. The curves, too, are suggestive of the possible activity of two discharging centers, the one fast and bilateral, the other slow and limited in its action to the leg which the subject was instructed to kick. These two phases of the voluntary reaction may differ also introspectively. It is conjectured that the fast part of the reaction gives the feeling of automaticity, being described by one subject as energy traveling directly across the cord, and that the slower phase may be connected with the reaction which the subject feels to be more strictly volitional.

(c) Reaction-time: Comparison of reaction-times of voluntary and conditioned responses must necessarily be done by an inspection of the distribution curves. The presence of two types of conditioned responses prevents a direct comparison of median values.

The distributions indicate that voluntary reaction-times are similar, on the whole, to the short-latency conditioned responses. When a ready signal is used, the voluntary reactions are uniformly fast, falling in the lower part of the distribution of short-latency conditioned responses. The voluntary reactions made while reading are slower. Their distribution is more nearly that of the short-latency conditioned responses than is that of the reactions with a ready signal. Figure VII shows the distribution of conditioned and voluntary responses made by Hir.

Although direct comparison of medians is unfruitful in the case of many subjects, the numerical values of the conditioning experiment have been included in Table VI along with the median values of the three categories of voluntary reactions studied.⁵⁷ In the cases of subjects Hir, Mon, San, Ste, Fje, and Harm the medians for the conditioned responses are high

⁵⁷ The medians for the conditioned responses are of the responses made only during the tests of the application of the "conditioned" stimulus. Pre-stimulation contractions in the double stimulations are obviously only the lower end of a distribution and cannot be used to determine the medians.

No reliabilities of differences are given (1) because of the small number of cases included in some of the figures and (2) because the inclusion of two types of responses makes such computations relatively meaningless. The P.E. of the differences is in some cases high because of the small number of cases, but ranges down to 1/20 of the difference.

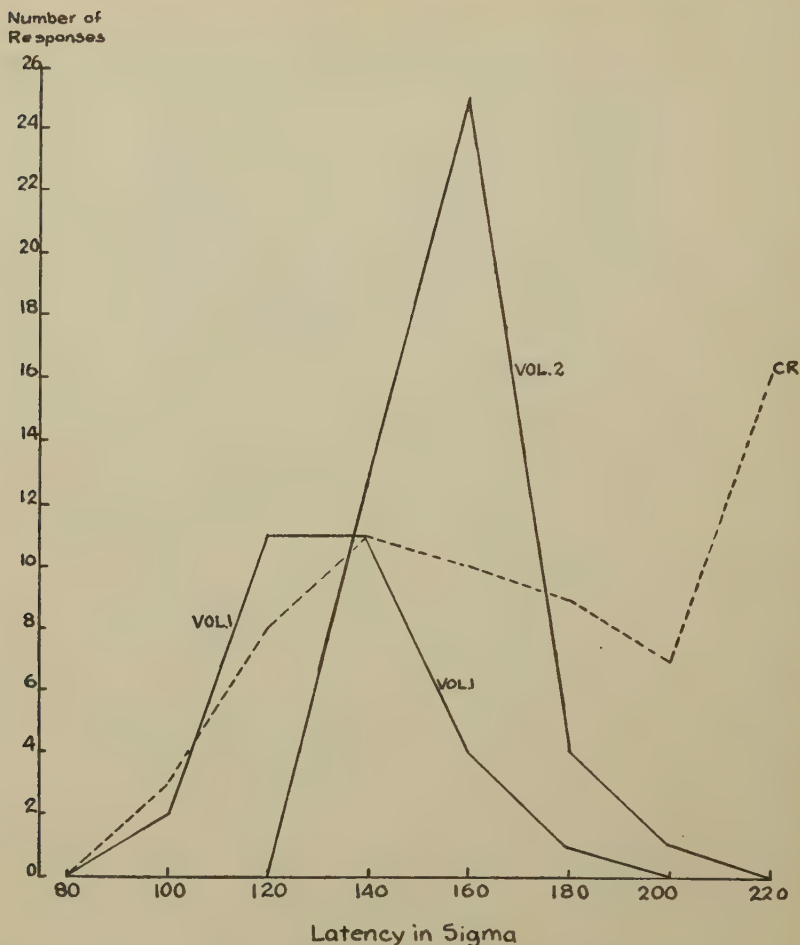


FIGURE VII. DISTRIBUTION OF LATENCIES OF CONDITIONED AND VOLUNTARY RESPONSES (SUBJECT HIR)

Cr—Pre-stimulation contractions given during the double stimulations in the conditioning period.

Vol. 1—Voluntary leg reactions to a blow on the opposite tendon. Ready signal used.

Vol. 2—Voluntary leg reactions to a blow on the opposite tendon. Subject's attention distracted by reading.

because of the inclusion of the long-latency responses. This raises the medians considerably above those for voluntary reactions. In the cases of subjects Rbw, Schu, and Asc direct comparisons can be made, since there was no evidence of long-latency conditioned responses in these subjects. By going behind the medians to the distributions which they represent, it

TABLE VI

Latencies in Sigma								
Subject		Conditioned responses	Vol. R. with ready signal	N	Vol. R. while reading	N	Vol. R. to sound cessation	N
Hir	25th % tile	210	113		140			
	median	247	122	29	150	45		
	75th % tile	275	135		160			
Mon	25th % tile	245	195		158			
	median	252	212	25	190	13		
	75th % tile	272	258		210			
San	25th % tile	268	135		188			
	median	307	145	30	204	62		
	75th % tile	350	158		221			
Rbw	25th % tile	120	122					
	median	140	130	36				
	75th % tile	150	147					
Ste	25th % tile	203	160		264		184	
	median	335	180	36	314	27	220	21
	75th % tile	345	211		375		251	
Lyo	25th % tile		127		248		136	
	median	182	148	31	365	21	166	14
	75th % tile		168		404		182	
Fje	25th % tile	178	132		156		179	
	median	205	139	30	170	30	182	25
	75th % tile	275	152		198		208	
Harm	25th % tile		105		138		141	
	median	260	116	26	168	21	148	18
	75th % tile		122		192		159	
Schi	25th % tile		132		219			
	median		142	37	490	8		
	75th % tile		167		640			
Schu	25th % tile	185	172		192		183	
	median	215	192	54	211	62	200	35
	75th % tile	225	203		230		230	
Asc	25th % tile	132	129		140			
	median	144	135	59	153	49		
	75th % tile	161	143		190			
Mad	25th % tile	130†	129		149		140	
	median	131	138	52	190	27	180	17*
	75th % tile	146	152		211		200	
Lon	25th % tile		114		151		143	
	median	150†	119	29	193	29	161	24
	75th % tile		124		209		184	
Dur	25th % tile		122		178		194	
	median	182	141	26	212	26	213	23
	75th % tile		162		252		287	
Bro	25th % tile		135		222		203	
	median		145	22	246	28	236	26
	75th % tile		190		262		282	
Harr	25th % tile		130					
			149	38				
			156					

*Reaction-time to a touch on the opposite leg was measured with this subject. (25th % tile—141, median—153, 75th % tile—166, N—61.)

†Conditioned responses given during tests for facilitation. They therefore are not representative of the true distribution.

seems justifiable to regard the voluntary reactions as being closely similar in reaction-time to the short-latency conditioned responses. In most cases the voluntary reactions while reading could be used as being representative of the latency of the bilateral conditioned responses. The exceptions to this can be explained by lack of automaticity of the voluntary reactions of these subjects.⁵⁸

(d) Amplitude of the reflex response: It would be interesting to find, in voluntary response as in conditioning, a diminution in the reflex response to the blow on the tendon. The first effect of the instructions to make voluntary reactions was usually an increase in the amplitude of the knee-jerk of the leg stimulated. This increase is readily attributable to the tenseness of the subject. Since the subject continues more or less tense throughout the period of voluntary reactions, interpretation of the results meets with difficulty. In order to secure comparable results it would be necessary to record voluntary reactions over periods as long as was done in the case of conditioned responses. But, bearing in mind the difficulties of interpretation of the present results, we see evidence in the case of some subjects (Asc, Mad, Ste and Dur) that a reduction of the reflex response results from continued voluntary response to its stimulus.⁵⁹ These results, however, require confirmation by carefully controlled experiment before they can be seriously considered. If the amplitude changes are in line with the other similarities between voluntary action and conditioned responses, they may prove to show, too, a decrement on continued repetition.

B. Voluntary leg reactions to sound:

Voluntary leg reactions to sound are about 40 sigma slower than voluntary reactions to a blow on the tendon of the opposite leg. They also seem to lack the automaticity characteristic of these latter reactions. Whether they may be bilateral was not established. No bilateral responses to sound were detected, but this cannot be considered conclusive since all

⁵⁸ There is evidence that long voluntary reaction-time while reading is correlated with absence of facilitation of a contralateral response by the tendon stimulus (see results of Lyo and Schi).

⁵⁹ Dodge (1926) found no support for the drainage hypothesis when subjects made a voluntary finger movement to the stimulus eliciting the knee-jerk.

the subjects were well-practiced in reaction by the time the reactions to sound were recorded. In other respects the contraction-curves of reactions to sound seemed to be quite similar to those made to a tendon blow. The curves were carefully inspected for differences in recruitment speed, shape of curve, etc., but the results do not seem to warrant the conclusion that there is a characteristic difference. Although, on the whole, the responses to sound showed slightly less steepness of rise, the exceptions to this were of sufficient frequency to make unwise a conclusion that there was a real difference. In view of the great variability of voluntary reactions, the evidence is by no means conclusive.⁶⁰

The reactions to sound do not seem to show a fast and a slow phase as was found in some of the responses to the stretch stimulus. This might be due to absence of the rapid automatic responses such as followed tendon stimulation. But this difference, too, might prove to be unreal if reactions to sound were studied more intensively.

C. *Voluntary reactions to touch:*

In the case of subject Mad an attempt was made to record voluntary reactions to a blow at the knee which would not result in muscle stretch but would retain the other tactual-kinesthetic stimulation present when the tendon is struck. This was partially achieved by allowing the percussion hammer to strike a wooden guard strapped over the leg and covering the tendon. The contraction-curves of response to this stimulus were similar to those of other voluntary reactions. The reaction-time was greater than in the case of the tendon stimulus and less than that to sound. The medians were: tendon stimulus—138 sigma, tactual stimulus—153 sigma, sound stimulus—180 sigma.

Discussion of Results

A comparison of the results of the voluntary reaction experiment with the results of the conditioned response experiment is in general confirmatory of past work. There is in

⁶⁰ In a preliminary investigation their similarity to conditioned responses to sound was also indicated. Conditioned responses to sound were developed and the contraction-curves recorded, but no measurements of latency were made.

these results, however, the clear implication that the facts are more complex than previous discussions have stated them. It was found that the speed of a conditioned response was very close to that of a voluntary reaction when the conditions under which each occurred were comparable. The condition of readiness for reaction was found to raise the excitability of the centers mediating the response so that the median latency of such reactions was typically below that of the conditioned responses made with attention distracted. The differences between the two are thus explicable in terms of degree of attentional adjustment. The results are further complex in indicating that the voluntary kick and the conditioned kick may both involve reactions of more than one central mechanism each of which gives a different character of response.

The character of the reactions to sound indicates—but does not prove—that the voluntary reaction to sound stimulation is similar to that made to tendon stimulation. The very short reaction-times of the voluntary response to the muscle stretch, when compared to the longer reaction-time to sound, could be considered as suggesting two different mechanisms. The greater automaticity of the former reactions adds to such likelihood. But, in view of the failure to find an essential difference in the objective character of the two reactions, the conclusion seems necessary for the present that the difference between them is only in closeness of the functional connections between stimulus and response.

A further discussion of the relations of voluntary reactions, conditioned responses and facilitation effects appears in the next section.

Conclusion

Although voluntary reactions were found to have greater range than conditioned responses, no essential differences between the two kinds of response were revealed.

SECTION VII. INTERPRETATION

The interpretation of the results of the present investigation meets with great difficulty at almost every point. Physiological theory concerning the knee-jerk has not advanced to such a stage that conclusions can be stated with confidence. It has already been pointed out in the preceding sections that in the case of almost every phenomenon described the results are open to a variety of explanations. Which of several possibilities is the true one cannot be stated until the available evidence is much extended.

The results can be made comprehensible, however, only by an attempt at their interpretation. In this section, therefore, certain mechanisms are suggested that seem to the writer best fitted for the explanation of the varied phenomena.

Conditioned Responses

The best interpretation of the two conditioned responses described is that they are two different phenomena. The short-latency bilateral response should be classed as an experimentally produced crossed reflex of the same kind as is found in certain abnormal conditions and in an occasional normal individual. The discharge which gives rise to it after conditioning is an augmentation of impulses which are normally subliminal for crossed response. This discharge is ordinarily revealed by its facilitating influence on crossed response and by the delayed relaxation of the quadriceps during the knee-jerk. Its level of action is most probably that of other automatic movements which research at present indicates to be mediated by cerebellar or mid-brain mechanisms. The long-latency response, on the other hand, is a "true" conditioned response due to an integration effected on the highest levels of the central nervous system. Whereas, in the case of the shorter-latency response there is an original integration of stimulus and response, in the case of the long-latency response the integration is essentially new. The characteristics of the latter response probably do not differ from a conditioned leg response to a sound, a light or a touch stimulus. In the case of such stimuli reflex connections with quadriceps contraction are

not close, and integration is effected more readily in the "association centers" of the cerebrum than in the lower levels.

The results point to the short-latency bilateral response as being of reflex origin.⁶¹ The fact that it is occasionally present in a normal individual and in abnormal conditions should alone be sufficient proof. Added evidence is the presence normally of marked facilitation of a contralateral response. The speed of development of the response under conditioning further points to this conclusion. A single combined stimulation was in one case sufficient to complete the integration. The probable negative adaptation of its crossed component seems to mark it off from other conditioning phenomena which are ordinarily improved by repetition of double stimulations. The resistance of the homolateral secondary response to attempted extinction shows the presence of an integration whose closeness is more characteristic of reflex connections than of the unstable conditioned response. Its low latency marks it off as a low-level adjustment such as is typically found in responses which require emergency measures to compensate for sudden environmental changes. And finally, the bilaterality of the discharge puts it under the category of reflexes. The conditioned response under the conditions used here should appear only as a kick of the second responding leg. Other reflexes are of this bilateral type, the lid-reflex to sound stimulation being an example.⁶²

It has already been pointed out in Section V that the development of the short-latency response by the conditioning technique calls for explanation on the basis of no essentially different process than the development of the long-latency conditioned response. Current theories of conditioning are applicable to either, the difference being merely in the close-

⁶¹ By "reflex" is here meant only that the neural connections are already present.

⁶² It is the guess of the writer that if Cason's stimulus-response situation of a sound plus a shock below one eye were modified so that the sound preceded the shock, two kinds of conditioned response would develop analogous to those found in the present investigation. The first would be a fast bilateral response due to a lowered threshold of the reflex to sound. The second would be a "true" conditioned response in which closure of only that eye which received the shock would be involved. This would be a response of long latency and would probably involve other facial muscles than those closing the lid. If this were the case, the short-latency wink would be analogous to the short-latency bilateral kick and the long-latency response to the unilateral kick of the leg receiving the unconditioned stimulus.

ness of the original integration. The conditioning of the bilateral response meets with relatively slight resistance, while the original connection at higher levels is less close. Although the difference between the two can be reduced to a matter of degree, it is probably best to keep them separate, classifying the short-latency response as a sensitization of a reflex arc which normally has a resistance high enough to prevent crossed response.

The long-latency response looks like the only "true" conditioned response developed. It has the characteristics of adaptation to the situation. The response was always limited to the leg which received the unconditioned stimulus. Its latency seemed adjusted to the stimulus interval.⁶³ It developed slowly, the first such response occurring only after 46 to 316 double stimulations. This points to an integration effected on a level where the original alliance of stimulus and response is slight.⁶⁴ The response increased in frequency with repetition of the combined stimulations, and continued to appear throughout the sittings. Its adaptation to the situation was further shown by its rapid disappearance on discontinuance of the double stimulations. Past work on conditioning has localized integrations of this type in the highest neural centers.

Voluntary Responses

The similarity of the voluntary reactions, conditioned responses and facilitation effects presents a problem for an explanation of the conditioning phenomena which is based on two levels of action. From the results alone it is necessary to make either of two assumptions. We may assume either that the level of the discharging center giving rise to conditioned responses is the same as that concerned in the initiation of voluntary activity, or that the centers concerned with volun-

⁶³ In the case of subject Hir the reflex response to the second blow came 245 sigma or more after the first stimulus. The long-latency conditioned responses had a median latency of 255 sigma. There is no conclusive evidence in the results for or against the notion that the latency of the responses is determined by the stimulus interval used. However, the results of the facilitation experiment where time interval could not be a factor indicated 300 to 400 sigma as about the upper limit at which we should expect to find conditioned responses. For the short-latency responses on the other hand the facilitation experiment is conclusive evidence that their latency is not determined by the stimulus interval.

⁶⁴ It further indicates a stimulus of low intensity.

tary activity have at least a part of their effect by raising the excitability of lower centers so that the responses may be mediated by them.

The data are best interpreted by attributing a dual effect to volition. One of these results is indirect, the other direct.

The results seem to show that the instructions to make voluntary reactions not only cause the subject to respond with truly voluntary kicks but also sensitize the reflex arcs which give rise to a more rapid and automatic bilateral kick. The decision of the subject to kick and the turning of his attention in anticipation of the blow is regarded as making possible a reflex kick of the same kind as that occurring as a conditioned bilateral response or subliminally as a facilitation effect. The response, both introspectively and objectively, shows characteristics of automaticity which mark it off from purely voluntary action.⁶⁵ But a truly volitional kick seems to be also present in the voluntary response. In the records of the experiment this appears as a secondary response after a faster bilateral response. The impulses which give rise to it probably originate in the highest centers, and the response exhibits those characteristics of greater range and better control—being unilateral—which mark off voluntary from reflex activity. It is further different in its subjective aspect, appearing to the subject as a response he has initiated.

The above interpretation amounts to saying that not all voluntary activity is actually voluntary. To a certain extent this is true, as the results of reaction-time experiments⁶⁶ and of everyday observation of habitual acts will readily reveal. In the present instance the instructions to the subject to react voluntarily are no guaranty that his future reactions will actually be wholly voluntary. We may take an analogy from the reflex wink of the eyelids to sound. By voluntary direc-

⁶⁵ Volition may achieve such a sensitization of the reflex arc by giving rise to continuous impulses which summate with the afferent impulses set up by the muscle stretch so as to cause response. There may be a functioning connection between the afferent impulses from the muscle and the fast bilateral response, but one with a resistance so high that the summation effect of impulses from the volitional centers is required to overcome it.

The theory of inhibitory release explains the facts equally well. See Fulton (1926) for a discussion of this theory.

⁶⁶ The Exner-Cattell conception of responses in reaction-time experiments as due to a holding in readiness of the reflex arc has been utilized in the interpretation of the present results.

tion of the attention in anticipation of a sudden sound of low intensity it is possible to provoke a lid-reflex of typically low latency. By a further exercise of volition it is possible to superimpose on this reflex a voluntary wink with a reaction-time almost three times that of the reflex. Both responses may be regarded as being due to volition, but the first is an indirect effect, the second a direct effect. The analogy of the lid reaction holds for the kick of the legs. The decision to kick and the direction of the attention in anticipation of the blow on the leg so sensitize the reflex centers that the response becomes possible through them. Added to this reflex response there may then be a true voluntary kick which differs from the reflex kick in reaction-time, in degree of control and in its subjective accompaniments. The impulses which give rise to it have their origin in the highest levels, while those giving rise to the bilateral response are the result of lower-level reflex connections.

An apparent obstacle to this explanation is the fact that the results failed to establish an essential difference between voluntary reactions to a blow on the tendon and voluntary reactions to sound stimulation. The first of these was shown to have intimate reflex connections with the response of the other leg, while in the case of sound stimulation such close integration seems less likely. If we assume that the incomplete results here described for the reactions to sound give a correct picture, the results can still be explained. Sudden sound stimulation is known to cause a generalized start-reaction which affects other muscle groups than those of the eye-lids. This response may, under favorable conditions, involve quadriceps contraction. The lack of a difference between reactions to sound and to a blow on the tendon would then be due to reflex connections between the auditory receptors and the quadriceps effectors, but connections of such high resistance that strong stimulation or facilitation as by summing impulses due to volition are necessary for response.⁶⁷

⁶⁷ The use of a very loud sound, producing a start-reaction, as a conditioned stimulus with the knee-jerk might also show two types of conditioned responses. The first would be fast, due to reflex connections; the second would be slow, the result of higher level integration. When using sound stimuli of ordinary intensity it may be that the easiest integration is the higher level one.

Facilitation Effects, Conditioned Responses and Voluntary Reactions

The preceding interpretation of the results brings all the phenomena into a coordinated scheme. It looks upon volition and conditioning as being alternate means of sensitizing a reflex arc which is in most normal individuals functional only to the extent of causing facilitation of a contralateral response. This arc may mediate a response either because of a lowering of threshold within the arc, as by conditioning or in habit formation, or by the aid of summing impulses, as in volitional activity or in some conditions of hyperreflexia. On the other hand, volition and conditioning are also looked upon as being alternate means of affecting that higher level integration which causes the long-latency responses. When such long-latency responses come during a reflex response to a stimulus, they show as facilitation of that response. They show as conditioned responses when, after prolonged combined applications, the second stimulus is omitted. In voluntary reactions they appear as those reactions which are of long reaction-time and of lesser automaticity. Whether the long-latency conditioned responses are due to a discharge of the same origin in the central nervous system as are the voluntary responses, cannot be stated, but the probability is strong that the same level is functional in each.

Physiology of the Knee-Jerk

The results of the present investigation seem to be additional definite evidence that the normal knee-jerk is the result of the activity of more than one level of the central nervous system. If we bear in mind that the end-effect of the knee-jerk is not the muscle contractions here recorded, but a change in the position of the lower leg, it is clear that responses spread over a considerable interval of time will result in an addition to the extent of movement. The final effect of three volleys of impulses arriving respectively from the fastest reflex center, the slower bilateral center and the highest automatic or volitional centers would result in a smooth movement with little of the discontinuity present in the records of muscle thickening.

The likelihood is strong that the bilateral response here described is due to an exaggeration of a discharge which has as

its homolateral representative the hump on the descending limb of the contraction-curve and in part accounts for the so-called "tonic" phase of the knee-jerk. The conditioning method, as used in the present investigation, is therefore a method for the exaggeration and isolation—because of the dropping out of the fast reflex in some cases—of this part of the tonic component of the knee-jerk. So far as the results go, they indicate that this part of the knee-jerk is not really tonic, but that it is a phasic reaction with characteristics not essentially different from other reflex responses. Its apparent tonic action is probably attributable to its incidence in the period of refractoriness following the faster response. However, interacting with and obscuring the discharges from such delay paths there is probably also a certain amount of contraction due to reflex stimulation from the rapid relaxation of the muscle.

The cooperation of the long-latency response in the production of the normal knee-jerk is likely. Past studies have shown augmentation of the knee-jerk as a result of sensory stimulation of all kinds. These stimuli in many instances have no direct reflex connection with quadriceps contraction, so we can most easily attribute the facilitation found to impulses mediated by the highest centers. There is reason to suppose that the blow to the knee also has high-level representation which, under the present circumstances, resulted in a conditioned response of long-latency and which, under normal conditions, adds further contraction to the normal knee-jerk. Contraction-curves clearly showing the arrival of three such volleys of impulses at one quadriceps were obtained in this investigation by properly manipulating the experimental conditions.

Amplitude Changes

The changes in the amplitude of the fast reflex response offer the greatest difficulty of interpretation. Although the writer is at present unprepared to advance a theory for this reduction in amplitude, the results were sufficiently clear to leave no doubt of their validity. The results seem to necessitate an explanation in terms of drainage. The drainage hypothesis is at present not favored by physiologists. However, the facts of conditioning and the facts of dominance of certain reaction patterns over others have led some to regard drain-

age as a necessary hypothesis. The facts in this case are objectively in line with drainage, but whether the mechanism of the adjustment is as conceived by McDougall, Pavlov and others is an open question.

Implications for Theory of Conditioning

The present results show that the phenomena of conditioning are sometimes more complex than past publications have described. In the results there are several warnings for future investigators.

1. Some subjects will probably not develop positive conditioned responses because the effect of the conditioned stimulus is inhibitory.

2. When there is originally a close integration of the conditioned stimulus with the unconditioned response, two types of conditioning are possible; the one a sensitized reflex making use of the integrational paths already present, the other a true conditioned response resulting from higher level integrations. The relative ease with which each appears is probably related to the stimulus interval used.

3. The comparison of voluntary reactions, conditioned responses and facilitation effects should be undertaken only when the conditions under which each is studied are the same.

4. The reduction in the original response to the conditioned stimulus and possibly also to the unconditioned stimulus is a significant accompaniment of the conditioning process.

5. The results of the present investigation seem clearly to imply that the word "conditioning" applies to an experimental method rather than to a functional process distinct from others. If the word is to be used for the process, it becomes necessary, because of objective similarities, that we bring under this category those processes which are tied up with voluntary activity. Voluntary reactions and habits resulting from them were found to be indistinguishable from similar responses due to conditioning alone. Whether one is willing to bring such modifications of behavior under the category of conditioning depends upon his bias. But, in view of the fact that many understand conditioning to apply only to processes in which volition does not operate, it seems more prudent and

less confusing to avoid for the present the extension of the term beyond the results of the experimental method known as conditioning. If future research continues to point to the similarity of conditioned responses with voluntary reactions, it may be that conditioning will be recognized as being the more fundamental process and that the term will be used to cover all these phenomena.

SUMMARY

An analytical study of conditioned responses was made. The stimuli used were successive blows at 1/5 second interval to the patellar tendon of each leg. In this situation integration of the first stimulus and the second response is theoretically possible on more than one level of the central nervous system.

Repeated successive stimulation by two blows is found to result in two kinds of conditioned responses due to integration on two levels.

One kind of response is a conditioned kick of the second responding leg on the omission of the second blow. It develops only after prolonged double stimulation and is easily extinguished. Its latency is typically 200 to 300 sigma. The integration is probably on a high level.

Another kind of response is due to the increase by double stimulations if a lower level integration which is normally already present between the stimulus to one quadriceps and the response of the other. Before conditioning this integration is revealed by the strong facilitating effect of a blow to one tendon on the response of the opposite leg and, in an occasional individual, by a crossed extension reflex normally present. The response due to the increase of this integration is bilateral, the stimulated muscle showing a secondary response coincident with the response of the other leg. Repetition of the double stimulations increases the homolateral secondary response more than the crossed response. The homolateral response is very resistant to extinction, but the crossed response is rapidly lost when single stimuli are given. The latency of the response is typically 120 to 180 sigma.

Voluntary leg reactions to a blow on the tendon have no essential differences from conditioned leg responses. There is evidence that in volition, as in conditioning, there are two levels of integration between the blow to one tendon and the response of the other leg. The one is a high-level integration which results in a response similar to the long-latency conditioned response; the second is a low-level integration which results in a fast bilateral response like the low-latency conditioned response. The latter is introspectively very automatic, while the former is introspectively volitional.

After making voluntary leg reactions to a blow on the tendon the subject will make automatic responses of the opposite leg on single stimulations. Such "habits" are in no way different from conditioned responses.

In some subjects the fast reflex knee-jerk is much reduced as a result of conditioning.

LITERATURE

- Adrian, E. D. 1926. The Impulses Produced by Sensory Nerve Endings. *J. Physiol.* 61, 49-72.
- Adrian, E. D. & Zotterman, Y. 1926. The Impulses Produced by Sensory Nerve Endings. *J. Physiol.* 61, 151-171.
- Anrep, G. V. 1923. The Irradiation of Conditioned Reflexes. *Proc. Roy. Soc.* 94B, 404-425.
- Austregesilo, A. 1928. Synreflexia (Association of Reflexes). *J. Nerv. Ment. Dis.* 68, 1-10.
- Beritoff, J. S. 1924. On the Fundamental Nervous Processes of the Cortex of the Cerebral Hemispheres. I. The Principle Stages of the Development of the Individual Reflex: its Generalization and Differentiation. *Brain* 47, 109-148.
- Böhme, A. 1927. Klinische Wichtige Reflexe. *Hdbch. d. Norm. u. Path. Physiol.* 10, 972-1017.
- Borovski, V. 1929. An Attempt at Building a Theory of Conditioned Reflexes on Spinal Reflexes. *J. Gen. Psychol.* 2, 3-11.
- Bowditch, H. P. & Warren, J. W. 1890. The Knee-Jerk and its Physiological Modifications. *J. Physiol.* 11, 25-64.
- Bremer, F. 1922. Sur un Reflex d'Extension de la Grenouille Spinale. *Arch. Intern. Physiol.* 19, 183-188.
- Brock, S. & Wechsler, I. S. 1924. Involuntary Movements: Their Unusual Association and Relation to the Phenomena of Decerebrate Rigidity. *Arch. Neurol. Psychiat.* 11, 698-706.
- Brown, G. 1915. Studies on the Physiology of the Central Nervous System. *Quar. J. Exper. Physiol.* 9, 81, 116-117, 140.
- Burr, C. W. 1921. Reflexes in Early Infancy. *Amer. J. Dis. Children* 21, 529-533.
- Cason, H. 1922. The Conditioned Eyelid Reaction. *J. Exp. Psychol.* 5, 153-196.
- Cason, H. 1923. A Note on the Conditioned Eyelid Reaction. *J. Exper. Psychol.* 6, 82-83.
- Cobb, S. 1925. Review on the Tonus of Skeletal Muscle. *Physiol. Rev.* 5, 518-550.
- Cooper, S. 1929. The Relation of Active to Inactive Fibres in Fractional Contraction of Muscles. *J. Physiol.* 67, 1-13.
- Cooper, S., Denny-Brown, D. E. & Sherrington, C. S. 1926. Reflex Fractionation of a Muscle. *Proc. Roy. Soc.* 100B, 448-462.
- Cornil, L. & Goldenfoun, Z. 1928. Sur une Nouvelle Methode d'étude des Reflexes Associatifs chez l'Enfant: les Reflexes Tendineo-Associatifs. *C. r. Soc. Biol.* 99(1), 408-409.
- Denny-Brown, D. E. 1929. On the Nature of Postural Reflexes. *Proc. Roy. Soc.* 104B, 252-301.
- Denny-Brown, D. E. & Liddell, E. G. T. 1927. The Stretch Reflex as a Spinal Process. *J. Physiol.* 63, 144-149.
- Dodge, R. 1911. A Systematic Exploration of the Normal Knee-Jerk, its Technique, the Form of the Muscle Contraction, its Amplitude, its Latent Time and its Theory. *Zsch. f. allg. Physiol.* 12, 1-58.
- Dodge, R. 1926. Theories of Inhibition. *Psychol. Rev.* 33, 106-122, 167-187.
- Dodge, R. 1926. The Problem of Inhibition. *Psychol. Rev.* 33, 1-12.
- Dodge, R. 1927. Elementary Conditions of Human Variability. C. U. Press, N. Y. 107 p.

- Dodge, R. & Benedict, F. G. 1915. Psychological Effects of Alcohol. Carnegie Instit. of Washington. 281 p.
- Eccles, J. C. & Granit, R. 1929. Crossed Extensor Reflexes and Their Interaction. *J. Physiol.* 67, 97-118.
- Erofeeva, M. 1912. Electrical Stimulation of the Skin of the Dog as a Conditioned Salivary Stimulus. Thesis, St. Petersburg.
- Fearing, F. 1930. Reflex Action. Baltimore, Williams & Wilkins. 350 p.
- Forbes, A. 1922. The Interpretation of Spinal Reflexes in Terms of Present Knowledge of Nerve Conduction. *Physiol. Rev.* 2, 361-414.
- Fulton, J. F. 1926. Muscular Contraction and the Reflex Control of Movement. Baltimore, Williams & Wilkins. 644 p.
- Golla, F. & Cook, L. C. 1929. An Isometric Study of the Human Knee and Ankle Reflexes. *Sir Fred. Mott Mem.* Vol. 45-56.
- Golla, F. & Hettwer, J. 1922. Time Relations of Tendon Reflexes in the Human Subject. *Proc. Roy. Soc.* 94B, 92-98.
- Gotch, F. 1896. Note on the So-Called Tendon Reflex. *J. Physiol.* 20, 322-333.
- Hamel, I. A. 1919. A Study and Analysis of the Conditioned Reflex. *Psychol. Monog.* 27, No. 188. 65 p.
- Hawthorne, C. O. 1914. On the Occurrence of Bilateral Extensor Response in States of Unconsciousness. *Practitioner* 93, 330-338.
- Hoffmann, P. 1922. Untersuchungen über der Eigenreflexe (Sehnenreflexe) Menschlicher Muskeln. Berlin. Springer. 106 p.
- Horax, G. 1921. Contributions of the War to the Physiology of the Nervous System. *Physiol. Rev.* 1, 269-294.
- Howell, H. W. 1925. Inhibition. *Physiol. Rev.* 5, 161-181.
- Humphrey, G. 1927. The Effect of Sequences of Indifferent Stimuli on a Reaction of the Conditioned Response Type. *J. Abn. Psychol.* 22, 194-212.
- Jacobson, E. 1928. Differential Relaxation During Reading, Writing and Other Activities as Tested by the Knee-Jerk. *Amer. J. Physiol.* 86, 675-693.
- Jacobson, E. 1929. Progressive Relaxation. Univ. of Chicago Press. 429 p.
- Lang, J. & Olmsted, J. M. D. 1923. Conditioned Reflexes and Pathways in the Spinal Cord. *Amer. J. Physiol.* 65, 603-611.
- Langworthy, O. R. 1928. The Control of Posture by the Central Nervous System. *Physiol. Rev.* 8, 151-190.
- Liddell, E. G. T. & Sherrington, C. S. 1923. Stimulus Rhythm in Reflex Tetanic Contraction. *Proc. Roy. Soc.* 95B, 142-157.
- Liddell, E. G. T. & Sherrington, C. S. 1924. Reflexes in Response to Stretch (Myotatic Reflexes). *Proc. Roy. Soc.* 96B, 212-242.
- Lombard, W. P. 1888. The Variations of the Normal Knee-Jerk and Their Relation to the Activities of the Central Nervous System. *Amer. J. Psychol.* 1, 5-71.
- Luciani, L. 1915. Human Physiology. Translated by F. A. Welby. London. McMillan. Vol. III. 667 p.
- Magnus, R. 1924. Körperstellung. Berlin. J. Springer. 740 p.
- McCouch, G. P. & Alpers. 1929. Extensor Reflexes from the Knees in Relation to the Knee-Jerk and to Rebound. *Arch. Neurol. Psychiat.* 22, 672-685.
- Olmsted, J. M. D. & Warner, W. P. 1922. Latent Period in Reciprocal Action of Antagonistic Muscles. *Amer. J. Physiol.* 59, 480.
- Pachon, V. & Petiteau, C. 1922. Sur la Non Spécificité du Caractère Bifide de la Secousse Reflexe Patellaire. *C. r. Soc. Biol.* 86, 542-545.

- Pike, F. H. 1909. Studies in the Physiology of the Central Nervous System. I. The General Phenomena of Spinal Shock. *Amer. J. Physiol.* 4, 124-152.
- Rademaker, G. G. J. 1926. Die Bedeutung der roten Kerne, etc. Berlin. Springer. 340 p.
- Razran, H. S. 1930. Theory of Conditioning and Related Phenomena. *Psychol. Rev.* 37, 25-43.
- Riddoch, G. 1917. On the Reflex Functions of the Completely Divided Spinal Cord in Man, Compared with Those Associated with Less Severe Lesions. *Brain* 40, 264-402.
- Riddoch, G. & Buzzard, E. F. 1922. Reflex Movements and Postural Reactions in Quadriplegia and Hemiplegia, with Especial Reference to Those of the Upper Limb. *Brain* 44, 397-489.
- Russetzki, J. J. 1928. Untersuchungen über den Kniesehenreflex beim Menschen. I. Mitt. Der Normale Kniesehenreflex. *Arch. f. Psychiat.* 86, 37-56.
- Salman, A. 1929. Nouvelles Observations Cliniques et Experimentales sur les Mouvements Automatiques qui Suivent les Efforts Volontaires. *Rev. Neurol.* 36, 428-438.
- Schäffer, H. 1922. Über Sehnenreflexe und die Methodik ihrer Latenzzeitbestimmung. *Zeit. f. d. ges. Neurol. Psychiat.* 74, 605-615.
- Schlossberg, H. 1928. A Study of the Conditioned Patellar Reflex. *J. Exper. Psychol.* 11, 468-494.
- Schwartz, A. 1882. Zur Lehre der Haut- und Sehnenreflexe. *Arch. f. Psychiat. Nervenkrh.* 13, 621-657.
- Sherrington, C. S. 1906. The Integrative Action of the Nervous System, Yale Univ. Press, New Haven. 411 p.
- Sherrington, C. S. 1892. Notes on the Arrangement of Some Motor Fibres in the Lumbo-Sacral Plexus. *J. Physiol.* 13, 621-772.
- Sherrington, C. S. 1910. On Reciprocal Innervation of Antagonistic Muscles. 14. On Double Reciprocal Innervation. *Proc. Roy. Soc.* 81B, 249-268.
- Shevalev, E. A. 1926. The Associated Patellar Reflex. Sbornik Posvia-shchonny Vladimiru Mikhailovichu Bekhterevu K 40-Lyetiu Professorskoy Deyatel'nosti. p. 105-123.
- Snyder, C. D. 1910. The Latency of Knee-Jerk Responses in Man as Measured by the Thread Galvanometer. *Amer. J. Physiol.* 26, 474-482.
- Souques, A. & Chauvet, S. 1912. Inversion des Réflexes Tricipitaux, Réflexe Contralatérale du Quadriceps chez un Ancien Hémiplégique. *Rev. Neurol.* 20, 717.
- Spiegel, E. A. 1926. Der Zentrale Mechanismus der Statischen Innervation. *Klin. Wochenschr.* 5(1), 277-281.
- Spiegel, E. A. 1927. Der Tonus der Skelettmuskulatur. Berlin. Springer. 203 p.
- Stewart, P. 1897. Experimental Observations on the Crossed Adductor Jerk. *J. Physiol.* 22, 61-67.
- Strughold, H. 1926. Die Relativ Refraktäre Phase des Patellar-Reflexes. *Klin. Wochenschr.* 5, 2333.
- Strughold, H. 1928. Beiträge zur Kenntniss der Refraktärphasen der Eigenreflexe beim Gesunden Menschen. I. Mitt. Der Einfluss der Atembewegung auf der Patellar und Achilles Reflex. *Ztschr. f. Biol.* 88, 346-362.
- Switzer, St. C. 1930. Backward Conditioning of the Lid Reflex. *J. Exper. Psychol.* 13, 76-97.

- Tilney, F. & Pike, F. H. 1925. Muscular Co-Ordination Experimentally Studied in its Relation to the Cerebellum. *Arch. Neurol. Psychiat.* 13, 289-334.
- Travis, L. E. & Hunter, T. A. 1927. Muscular Rhythms and Action Currents. *Amer. J. Physiol.* 81, 355-359.
- Travis, L. E., Tuttle, W. W. & Hunter, T. A. 1927. Tetanic Nature of the Knee-Jerk Response in Man. *Amer. J. Physiol.* 81, 670-678.
- Travis, L. E. & Young, C. W. 1930. The Relations of Electromyographically Recorded Reflex Times in the Patellar and Achilles Reflexes to Certain Physical Measurements and to Intelligence. *J. Gen. Psychol.* 3, 374-400.
- Tuttle, W. W. 1925. Factors Influencing the Knee-Jerk. *Amer. J. Physiol.* 72, 50-55.
- Tuttle, W. W. 1925. The Distribution of Tone in Skeletal Muscle. *J. Exper. Psychol.* 8, 319-322.
- Tuttle, W. W. 1928. Rate of Conduction in the Reflex Arc. *Amer. J. Physiol.* 85, 409.
- Twitmyer, E. B. 1902. A Study of the Knee-Jerk. Philadelphia. Thesis—.
- Ufland, I. M. 1925. Das Hervorrufen des Beugenreflexes vom Rezeptivfeld des Abwischreflexes. *Pflüger's Arch.* 208, 87-92.
- Ukhtomski, A. 1911. The Dependence of Cortical Motor Reactions upon Adjacent Central Effects. *Transact. St. Petersburg Soc. Natur. Sci.* 41, Ser. 2, 179-393. German Abst. 393-412.
- Upton, M. 1929. The Auditory Sensitivity of Guinea Pigs. *Amer. J. Psychol.* 41, 412-421.
- Van Gehuchten, P. 1930. L'Abolition des Reflexes Tendineux dans les Tumeurs du Vle Ventricle. Contribution a l'Étude du Mécanisme des Reflexes Tendineux. *J. Neurol. Psychiat.* 30, 201-213.
- Wachholder, K. 1923. Untersuchungen über die Innervation und Koordination der Bewegungen mit Hilfe der Aktionsströme. I. Die Aktionsströme Menschlicher Muskeln bei Willkürlicher Innervation. *Pflüger's Arch.* 199, 595-624.
- Wacholder, K. 1925. Über die Koordination der Agonisten und Synergisten bei Unseren Willkürlichen Bewegung. *Klin. Woch.* 4, 263-364.
- Walshe, F. M. R. 1914. The Physiological Significance of the Reflex Phenomena in Spastic Paralysis of the Lower Limbs. *Brain* 37, 269-336.
- Walshe, F. M. R. 1919. On the Genesis and Physiological Significance of Spasticity and Other Disorders of Motor Innervation: with a Consideration of the Functional Relationships of the Pyramidal System. *Brain* 42, 1-28.
- Walshe, F. M. R. 1923. On Certain Tonic or Postural Reflexes in Hemiplegia with Special Reference to the So-Called "Associated Movements." *Brain* 46, 1-37.
- Walshe, F. M. R. 1923. The Decerebrate Rigidity of Sherrington in Man. *Arch. Neurol. Psychiat.* 10, 1-28.
- Walshe, F. M. R. 1923. The Work of Magnus and His Collaborators on the Nervous Regulation of Posture, and its Bearing on Some Modern Neurological Problems. *Med. Sc. Abstr. Rev.* 7, 109-118.
- Walton, G. L. & Paul, W. E. 1906. The Cerebral Element in Reflexes, and its Relation to the Spinal Element. *J. Nerv. Ment. Dis.* 33, 681-691.
- Wegener, H. 1927. Der gekreuzte Adduktorenreflex. *Monatschr. Psychiat. Neurol.* 66, 342-355.
- Whitehorn, J. C. & Lundholm, H. 1930. The Relation Between Stature and the Latent Period of the Knee-Jerk. *Amer. J. Physiol.* 92, 214-222.
- Woodworth, R. S. 1929. Psychology. Revised Edition. N. Y. Holt. 509 p.

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